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# CONTENTS OF VOLUME 98

NUMBER 1

*OTUS PETERSONI*, A NEW SCREECH-OWL FROM THE EASTERN ANDES, WITH SYSTEMATIC NOTES ON *O. COLOMBIANUS* AND *O. INGENS* ..... *John W. Fitzpatrick and John P. O'Neill* 1

MATING SYSTEM AND REPRODUCTIVE SUCCESS OF A SMALL POPULATION OF POLYGAMOUS SNOWY PLOVERS ..... *John S. Warriner, Jane C. Warriner, Gary W. Page, and Lynne E. Stenzel* 15

TEMPORAL DYNAMICS OF NEOTROPICAL BIRDS WITH SPECIAL REFERENCE TO FRUGIVORES IN SECOND-GROWTH WOODS ..... *Thomas E. Martin and James R. Karr* 38

STRUCTURE, SEASONAL DYNAMICS, AND HABITAT RELATIONSHIPS OF AVIAN COMMUNITIES IN SMALL EVEN-AGED FOREST STANDS ..... *Richard H. Yahner* 61

LATE SUMMER–SPRING MOVEMENTS OF JUVENILE SAGE GROUSE *Peter O. Dunn and Clait E. Braun* 83

ASSORTATIVE MATING AND SEXUAL DIMORPHISM IN THE COMMON TERN ... *Malcolm C. Coulter* 93

RUDDY TURNSTONES, GREAT HORNED OWLS, AND EGG LOSS FROM COMMON TERN CLUTCHES *Ralph D. Morris and David A. Wiggins* 101

PREY-SIZE SELECTION IN NESTING MALE AND FEMALE COOPER'S HAWKS *Patricia L. Kennedy and Donald R. Johnson* 110

HUNTING SUCCESS OF SOME MISSOURI RAPTORS ..... *Brian Toland* 116

GENERAL NOTES

GROWTH OF SHINY COWBIRD AND HOST CHICKS ..... *James W. Wiley* 126

AUTUMN SANDHILL CRANE HABITAT USE IN SOUTHEAST OREGON ..... *Carroll D. Littlefield* 131

DIETS OF HOUSE SPARROWS IN URBAN AND RURAL HABITATS *Ann P. Gavett and James S. Wakeley* 137

VEGETATION STRUCTURE AND VESPER SPARROW TERRITORY LOCATION ..... *J. Michael Reed* 144

MALE AND FEMALE PARENTAL CARE IN TREE SWALLOWS ..... *Terry E. Quinney* 147

EXTRAPAIR COPULATIONS IN THE TREE SWALLOW ..... *Michael P. Lombardo* 150

POLYGYNY IN THE YELLOW WARBLER ..... *Dominick A. DellaSala* 152

TWO MALE BOBOLINKS FEED YOUNG AT THE SAME NEST ..... *Eric K. Bollinger, Thomas A. Gavin, Catherine J. Hibbard, and J. Timothy Wootton* 154

CONSPECIFIC NEST TAKEOVERS AND EGG DESTRUCTION BY WHITE IBISES ..... *Peter Frederick* 156

WINTER DIETS OF VULTURES IN SOUTHCENTRAL PENNSYLVANIA *Richard H. Yahner, Gerald L. Storm, and Anthony L. Wright* 157

BREEDING BIOLOGY OF THE SEYCHELLES BLACK PARROT (*CORACOPSIS NIGRA BARKLYI*) *Robert E. Merritt, Patricia A. Bell, Victorin Laboudallon* 160

ADDITIONS TO RECORDS OF NORTH AMERICAN AVIFAUNA IN YUCATÁN, MEXICO *David T. Rogers, Jr., Jesús Garcia B., and Antonio Rógel B.* 163

CHOICE OF NEST BOXES BY CAVITY-NESTING DUCKS *Harry G. Lumsden, Judy Robinson, and Ronald Hartford* 167

ROCK DOVES NESTING IN TREES ..... *A. Townsend Peterson* 168

A NEW METHOD FOR COLLECTING PREY DELIVERED TO TUFTED PUFFIN CHICKS ... *Pat Baird* 169

LAUGHING GULL NESTING ATTEMPT ON LAKE ERIE *Elliot J. Tramer and Louis W. Campbell* 170

ADULT MALE BLUE GROUSE EATS LIZARDS ..... *Lee H. Simons* 171

ORNITHOLOGICAL LITERATURE ..... 173

ANNOUNCEMENT ..... 100

ERRATA ..... 92

NUMBER 2

WAX DIGESTION IN WILSON'S STORM-PETREL ..... *Bryan S. Obst* 189

FORAGING PATTERNS OF FOREST BIRDS: MALE-FEMALE DIFFERENCES ..... *Richard T. Holmes* 196

THE STRUCTURE OF A FOREST BIRD COMMUNITY DURING WINTER AND SUMMER
*Michael L. Morrison, Kimberly A. With, and Irene C. Timossi* 214

NEST-SITE CHARACTERISTICS OF OPEN-NESTING BIRDS IN RIPARIAN HABITATS IN IOWA
*Dean F. Stauffer and Louis B. Best* 231

ASPECTS OF THE BIOLOGY OF THE HORNED SCREAMER IN SOUTHWESTERN COLOMBIA
*Luis G. Naranjo* 243

SOME ASPECTS OF THE BREEDING BIOLOGY OF RED-WINGED BLACKBIRDS IN ALASKA
*A. David McGuire* 257

AGE-SPECIFIC FORAGING ABILITY AND THE EVOLUTION OF DEFERRED BREEDING IN THREE SPECIES OF GULLS ..... *Alexis A. E. MacLean* 267

THE EFFECTS OF MUSCLE BIOPSY ON SURVIVAL AND CONDITION IN WHITE-THROATED SPARROWS
*David F. Westneat* 280

GENERAL NOTES

DISTRIBUTION OF FOOD WITHIN BROODS OF BARN SWALLOWS
*W. Bruce McGillivray and Howard Levenson* 286

SPECIES-AREA RELATIONSHIP OF MIGRANTS IN ISOLATED WOODLOTS IN EAST-CENTRAL ILLINOIS ..... *John G. Blake* 291

INCUBATION CONTINUITY AND THE ADVANTAGE OF CRYPTIC EGG COLORATION TO MOURNING DOVES ..... *David Westmoreland and Louis B. Best* 297

EFFECTS OF OLD NESTS ON NEST-SITE SELECTION IN BLACK-CROWNED NIGHT-HERONS AND SNOWY EGRETS ..... *William E. Davis, Jr.* 300

THE USE OF TAPE-RECORDED CALLS TO COUNT VIRGINIA RAILS AND SORAS
*Rex R. Johnson and James J. Dinsmore* 303

FOOD ROBBERY OF WINTERING RING-NECKED DUCKS BY AMERICAN COOTS
*James F. Bergan and Loren M. Smith* 306

POLYGYNY IN THE EVENING GROSBEAK ..... *Barbara A. Fee and Marc Bekoff* 308

NESTING TRIOS OF MOURNING DOVES ..... *David E. Blockstein* 309

SUPERNUMERARY ADULTS FEEDING WILLOW FLYCATCHER FLEDGLINGS
*Michael D. Stafford* 311

BROOD ADOPTION BY A MALE BLACK-CAPPED CHICKADEE ..... *James L. Howitz* 312

BROWN THRASHERS RESPOND TO CALLS OF NORTHERN MOCKINGBIRD NESTLINGS
*Kimberly G. Smith* 313

BEHAVIOR OF A POLYGYNOUS YEARLING YELLOW WARBLER
*Mary L. Reid and Spencer G. Sealy* 315

RANGE EXTENSION OF CAYENNE TERNS ON THE PUERTO RICO BANK
*Fred C. Schaffner, Robert L. Norton, and John Taylor* 317

DOWNY WOODPECKER FEEDS ON INSECTS IN A SPIDER'S WEB ..... *Harry M. Tiebout, III* 319

NEST-BUILDING BEHAVIOR IN A YOUNG AMERICAN ROBIN ..... *Pamela C. Rasmussen* 319

THE HISS-DISPLAY OF NESTLING BLACK-CAPPED CHICKADEES IN CAPTIVITY
*Karen M. Apel and Charles M. Weise* 320

NESTLING GREAT CRESTED FLYCATCHER PARASITIZED BY LARVAL FLY (*PROTOCALLIPHORA HIRUDO*) ..... *Barrett A. Garrison, Catherine Vouchilas, and Dean F. Stauffer* 321

ORNITHOLOGICAL LITERATURE ..... 322

ANNOUNCEMENTS ..... 195, 333

INFORMATION FOR AUTHORS ..... 335

NUMBER 3

A NEW SPECIES OF ANTWREN (FORMICARIIDAE: *HERPSILOCHMUS*) FROM PERU, WITH COMMENTS ON THE SYSTEMATICS OF OTHER MEMBERS OF THE GENUS
*Tristan J. Davis and John P. O'Neill* 337

NESTING SUCCESS AND PRODUCTIVITY OF HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA ..... *William H. Baltosser* 353

THE HISTORY OF THE SOUTHERN FLORIDA WOOD STORK POPULATION
*James A. Kushlan and Paula C. Frohring* 368

THE EVOLUTION OF REVERSED SEXUAL DIMORPHISM IN OWLS: AN EMPIRICAL ANALYSIS OF POSSIBLE SELECTIVE FACTORS ..... *Helmut C. Mueller* 387

WINTER POPULATION DYNAMICS OF THREE SPECIES OF MAST-EATING BIRDS IN THE EASTERN UNITED STATES ..... *Kimberly G. Smith* 407

SOCIAL ORGANIZATION, MOVEMENTS, AND HOME RANGES OF BLUE GROUSE IN FALL AND WINTER
*James E. Hines* 419

SUBSPECIES OF THE GREATER SCAUP AND THEIR NAMES ..... *Richard C. Banks* 433

FOOD CONSUMPTION AND GROWTH ENERGETICS OF NESTLING GOLDEN EAGLES
*Michael W. Collopy* 445

GENERAL NOTES

CLUTCH-SIZE DIFFERENCES IN WESTERN AND INTRODUCED EASTERN POPULATIONS OF HOUSE FINCHES: PATTERNS AND HYPOTHESES ..... *J. Timothy Wootton* 459

LATE FLEDGING DATES, RENESTING, AND LARGE CLUTCHES OF PRAIRIE FALCONS
*George T. Allen, Robert K. Murphy, Karen Steenhof, and Stephen W. Platt* 463

CHARACTERISTICS OF RED-SHOULDERED HAWK NESTS IN SOUTHEAST OHIO
*Mark S. Woodrey* 466

SPRIG DELIVERY BY BROAD-WINGED HAWKS
*David M. Lyons, Kimberly Titus, and James A. Mosher* 469

REVERSE MOUNTING IN THE AMERICAN KESTREL
*Reed Bowman and Elizabeth M. Curley* 472

INTRASPECIFIC BROOD PARASITISM IN THREE SPECIES OF PRAIRIE-BREEDING SHOREBIRDS
*Mark A. Colwell* 473

SUSPECTED INTRASPECIFIC EGG DUMPING IN THE WHITE IBIS (*EUDOCIMUS ALBUS*)
*Peter C. Frederick and Mark A. Shields* 476

A CASE OF BROOD MIXING BY COMMON LOONS
*Paul I. V. Strong, John A. Bissonette, and Richard Souza* 478

USE OF FENCEPOST CAVITIES BY NESTING EASTERN BLUEBIRDS IN SOUTHWESTERN VIRGINIA
*Thomas A. Pierson and Patrick F. Scanlon* 479

LITTLE BLUE HERONS NESTING AMONG CATTAILS
*Richard T. Hoppe and Robert A. Kennamer* 482

SWALLOWS TAKING INSECTS FROM POND SURFACES
*Robert R. Cohen and Mark L. Dymerski* 483

DRINKING BY NORTHERN BOBWHITES IN TEXAS ... *N. L. N. S. Prasad and Fred S. Guthery* 485

SEVERE AGGRESSION BETWEEN FEMALE BLACK-HEADED GROSBEAKS ..... *Geoffrey E. Hill* 486

AN ALBINO GREATER SHEARWATER: FEATHER ABRASION AND FLIGHT ENERGETICS
*David S. Lee and Gilbert S. Grant* 488

ORNITHOLOGICAL LITERATURE ..... 491

ANNOUNCEMENTS ..... 418, 504

NUMBER 4

OBSERVATIONS ON THE ECOLOGY AND BEHAVIOR OF THE PALE-BILLED SICKLEBILL
*Bruce M. Beehler and Carol H. Beehler* 505

POTENTIAL USE OF FEATHER CHEMISTRY AS AN INDICATOR OF RELATIVE GROWTH
*Gary R. Bortolotti and Jon C. Barlow* 516

TIMING AND LOCATION OF SPRING SPERM RELEASE IN NORTHERN THRUSHES ..... *W. B. Quay* 526

GROWTH OF NESTLING SAGE SPARROWS AND BREWER'S SPARROWS
*Kenneth L. Petersen, Louis B. Best, and Brian M. Winter* 535

NEST-SITE CHARACTERISTICS AND REPRODUCTIVE SUCCESS OF LONG-EARED OWLS IN SOUTHWESTERN IDAHO ..... *Jeffrey S. Marks* 547

RED-TAILED HAWK NEST SITES IN PUERTO RICO
*Eduardo Santana C., Eddie N. Laboy, James A. Mosher, and Stanley A. Temple* 561

THE COURTSHIP BEHAVIOR AND MIXED-SPECIES PAIRING OF KING AND IMPERIAL BLUE-EYED SHAGS (*PHALACROCORAX ALBIVENTER* AND *P. ATRICEPS*) ..... *Douglas Siegel-Causey* 571

GENERAL NOTES

DISPERSAL OF RECENTLY FLEDGED MOURNING DOVES FROM NEST SITES
*Ronald R. Hitchcock and Ralph E. Mirarchi* 581

OBSERVATIONS ON THE BREEDING BIOLOGY OF EMERALD TOUCANETS IN COSTA RICA
*Cecilia M. Riley* 585

SEABIRD DENSITIES AND AGGREGATIONS DURING THE 1983 EL NIÑO IN THE GALAPAGOS ISLANDS ..... *David Cameron Duffy and Godfrey Merlen* 588

COLOR VARIATION IN THE RUDDY DUCK (*OXYURA JAMAICENSIS ANDINA*) ..... *Jon Fjeldså* 592

SYSTEMATIC INTERPRETATIONS OF FOOT-SCUTE PATTERNS IN NEOTROPICAL FINCHES
*George A. Clark, Jr.* 594

NORTHERN HARRIER PREDATION ON WILLOW PTARMIGAN
*David S. Hik, Susan J. Hannon, and Kathy Martin* 597

PREDATION ON BLACK AND TURKEY VULTURES .... *John S. Coleman and James D. Fraser* 600

EASTERN BLUEBIRD RESPONSES TO NOCTURNAL BLACK RAT SNAKE PREDATION
*R. Craig Hensley and Kimberly G. Smith* 602

DESTRUCTION OF HETEROSPECIFIC EGGS BY THE GRAY CATBIRD
*Jean-Claude Belles-Isles and Jaroslav Picman* 603

FATAL ANTIPREDATOR BEHAVIOR OF A KILLDEER ..... *Dianne H. Brunton* 605

PLUNGE-DIVING BY OLIVACEOUS CORMORANTS IN CHILE ..... *David Cameron Duffy, Rory P. Wilson, Marie-Pierre Wilson, and Claudio Velasquez R.* 607

WHICH SEX LEADS IN PAIRED MALLARDS? ..... *Kim C. Derrickson* 608

AGES OF MATED PAIRS OF CALIFORNIA GULLS ..... *Bruce H. Pugesek and Kenneth L. Diem* 610

AERIAL RAIN BATHING BY COMMON NIGHTHAWKS
*Kevin J. McGowan and Glen E. Woolfenden* 612

GREEN-BACKED HERON BAITS FISH WITH INSECTS
*Charles R. Preston, Hershel Moseley, and Carolyn Moseley* 613

GREAT-TAILED GRACKLE KILLS BARN SWALLOW IN FLIGHT ..... *Roger B. Clapp* 614

ORNITHOLOGICAL LITERATURE ..... 616

PROCEEDINGS OF THE SIXTY-SEVENTH ANNUAL MEETING ..... *John L. Zimmerman* 626

ANNOUNCEMENTS ..... 534, 560, 625, 639

INDEX ..... 641

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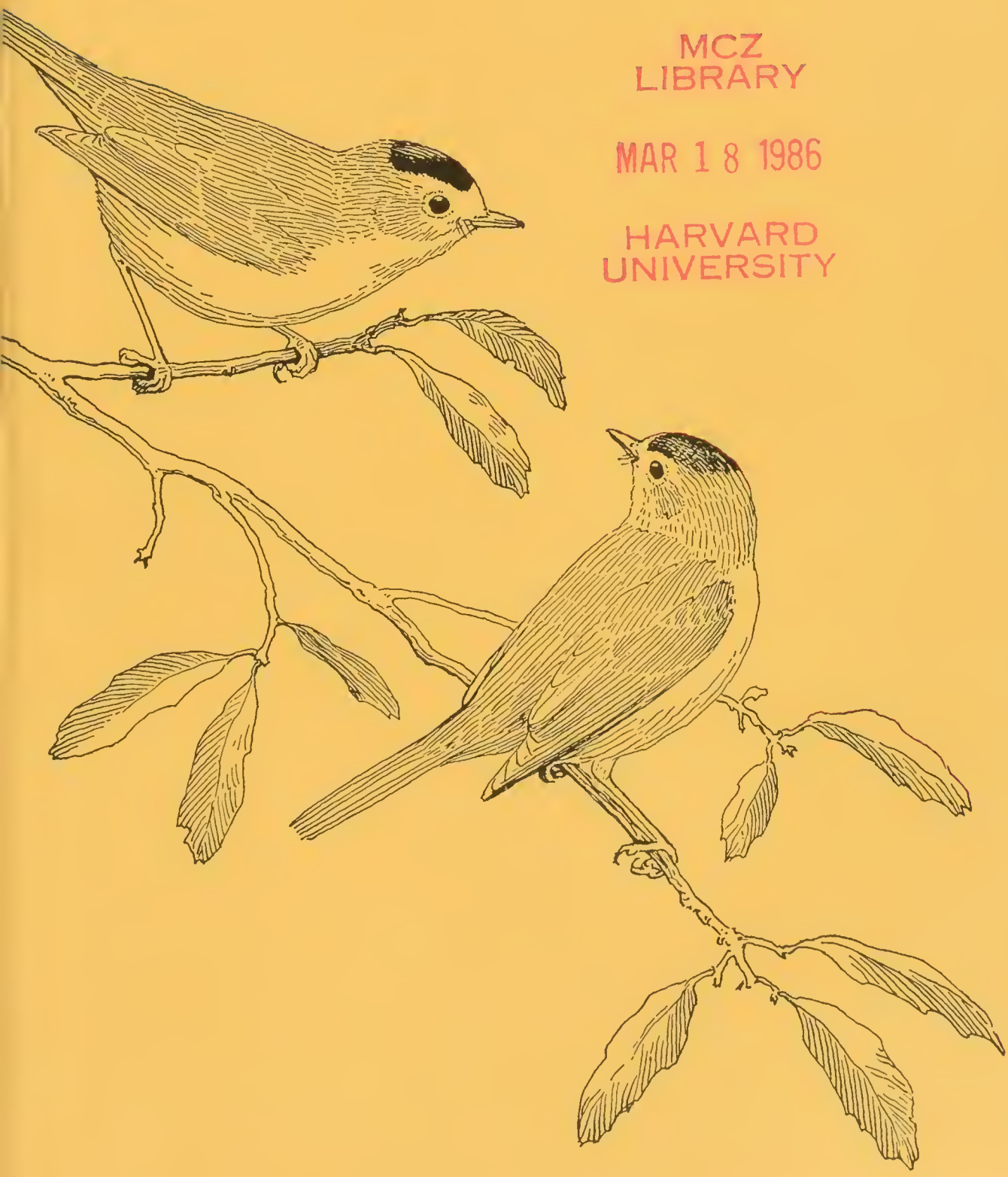

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Cinnamon Screech-Owl, *Otus petersoni*,
a new species from the eastern Andean cloud forest.
Painting by Roger Tory Peterson after whom the species is named.

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# *OTUS PETERSONI*, A NEW SCREECH-OWL FROM THE EASTERN ANDES, WITH SYSTEMATIC NOTES ON *O. COLOMBIANUS* AND *O. INGENS*

JOHN W. FITZPATRICK[1] AND JOHN P. O'NEILL[2]

ABSTRACT.—*Otus petersoni*, the Cinnamon Screech-Owl, is described and named in honor of Roger Tory Peterson. This small owl is now known from ten specimens and four localities in the cloud-forests of extreme northern Peru and southern Ecuador. Its plumage variation, reproductive information, habitat and ecology, voice, and systematic relationships are discussed. The closest living relative of the new form appears to be *O. colombianus*, the Colombian Screech-Owl, until now thought to be a subspecies of *O. ingens* but recognizable as a distinct species, primarily by its large size and proportionately long, bare tarsi. We suggest that *petersoni* and *colombianus* are sister taxa within a species-group of brown-eyed forms, including two other Andean taxa (*ingens* and *marshalli*) and a lowland, Amazonian species (*watsonii*). The names "*aequatorialis*" and "*minimus*" are synonyms of nominate *ingens*. *Received 11 Nov. 1984, accepted 31 Oct. 1985.*

In 1976 a joint field party from Princeton University and Louisiana State University returned to the Cordillera del Cóndor, a mountain ridge in extreme northern Peru where two undescribed bird species had been discovered the previous year (Bar-winged Wood-Wren [*Henicorhina leucoptera*], and Royal Sunangel [*Heliangelus regalis*], Fitzpatrick et al. 1977, 1979). This second expedition proved equally rewarding, producing numerous southerly range extensions of known Ecuadorian forms (see Parker et al. 1985) and two additional undescribed species (including the Cinnamon-breasted Pygmy-Tyrant [*Hemitriccus cinnamomeipectus*], Fitzpatrick and O'Neill 1979). Here we describe the second of these new species, a small screech-owl (see Frontispiece) that has since been collected at three other sites in Peru and southern Ecuador. The species may even

[1] Bird Division, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Dr., Chicago, Illinois 60605.
[2] Museum of Natural Science, Louisiana State Univ., Baton Rouge, Louisiana 70803.

occur as far north as Colombia, based on the recent discovery by M. Robbins of an old "Bogota" specimen in the collection of the Academy of Natural Sciences of Philadelphia.

An investigation of the systematic relationships of the new species led us to discover that the form currently known as the Rufescent Screech Owl (*Otus ingens*) actually constitutes two full species, one of them endemic to the Pacific slope cloud forests of Colombia and Ecuador. Relationships in this species group and within *O. ingens* are discussed following our description of the new form.

## ***Otus petersoni*** sp. nov.

CINNAMON SCREECH-OWL

HOLOTYPE.—American Museum of Natural History No. 824049; adult male from the Cordillera del Cóndor, above San José de Lourdes, Dept. Cajamarca, Peru, 5°02′S, 78°51′W, elevation 1950 m; collected and prepared 17 July 1976 by John W. Fitzpatrick, field number 76-041.

DIAGNOSIS.—A small *Otus* characterized by warm buffy-brown plumage throughout, ear tufts of medium length, a narrow, buffy nuchal collar, nearly fully feathered tarsi, and dark brown irides. Strikingly similar in coloration to *Otus* "*ingens*" *colombianus* but much smaller (wing chord 153.0–165.5 mm versus 176.5–192.0 mm, Table 1), distal half of tarsus sparsely feathered nearly to toes instead of bare, legs and toes of dried specimens proportionately shorter and more slender, ear tufts less pronounced, facial disc slightly darker with more conspicuous blackish edges, and breast less vermiculated. Differs from *O. ingens* by much smaller size (Table 1), breast and belly feathers much less vermiculated, warm buffy-brown rather than dark brown dorsal plumage, and by complete absence of white on any body or wing feathers, the palest color on *petersoni* being a rich, warm buff. Best distinguished from *O. watsonii* (red phase is most similar) by sparse rather than ample feathering on distal portion of tarsus, and by ear tufts of short to medium length and buffy-brown instead of long, pointed, and blackish on most specimens of *watsonii*; also by generally warmer buff coloration, less conspicuous blackish edge of facial disc, and nasal and inter-orbital tufts pale buff, not blackish as in most *watsonii*. Best distinguished from the similar-sized *O. marshalli* by absence of large white spots, separated by dark transverse barring, on the underparts; also lacks the contrasting black rim around facial disc and the white scapular spots of *marshalli*.

DISTRIBUTION.—Forested eastern foothills of the Andes from southern Ecuador (Cordillera del Cutucú) south to northern Peru in the departments of Piura (Playón), Cajamarca (type locality), and Amazonas (12–20 km east of La Peca), at elevations between 1690 and 2450 m. Possibly the Andes of Colombia ("Bogota" trade skin).

DESCRIPTION OF THE HOLOTYPE.—Dorsal coloration cinnamon-brown, closest to Raw Umber (Color 223; capitalized colors from Smithe 1975, 1981) but slightly buffier; feathers of crown and dorsum finely vermiculated with double, wavy bars, alternating between dark brownish and paler, buffy brown, the distal darker bars breaking up into mottling on most feathers. Nuchal collar pale buff, these feathers tipped with one to three darker-brown bars. Crown only slightly darker brown than back, but lacking the soft buffy undercoat present throughout the dorsum. Ear tufts of moderate length (longest feather 29 mm), buffy at base and brownish, mottled blackish, toward tips. Scapulars largely unmarked, closest to pale Cinnamon (Color 123A), forming a row of rich, light buffy patches between dorsum

TABLE 1

MEASUREMENTS (MM) OF *OTUS PETERSONI*, *O. COLOMBIANUS*, AND *O. I. INGENS*[a]

| | Wing chord | Tail | Tarsus | Middle toe[b] | Culmen | Weight[c] |
|---|---|---|---|---|---|---|
| Males | | | | | | |
| *petersoni* (6) | 157.0 (153–165.5) | 85.6 (81–90) | 27.2 (25–29) | 20.2 (19–22) | 21.5 (21–22.5) | 97 (6) (88–119) |
| *colombianus* (4) | 181.5 (175–186) | 93.5 (90–96) | 35.8 (34–37) | 24.2 (23–25) | 25.4 (24–27.5) | 153 (2) (150–156) |
| *i. ingens*[d] (19) | 192.0 (183.5–200) | 101.2 (94–106) | 32.2 (31–34.5) | 24.8 (23.5–26) | 24.2 (23–26.5) | 154 (7) (134–180) |
| Females | | | | | | |
| *petersoni* (3) | 157.3 (155–161.5) | 86.8 (85–90.5) | 27.5 (26.5–29) | 19.3 (18–20) | 21.5 (21–22) | 98 (3) (92–105) |
| *colombianus* (5) | 181.2 (176.5–185) | 98.5 (95–103) | 34.2 (33–36) | 23.6 (23–24) | 24.8 (24.5–25) | "210" (1) (210) |
| *i. ingens*[d] (9) | 196.0 (188–208) | 106.1 (102–112) | 33.1 (32–34.5) | 25.5 (24–26) | 24.1 (23–25.5) | 182 (5) (140–"223") |
| Unknown sex | | | | | | |
| *petersoni* (1) | 165.0 | 85.0 | 29.0 | 19.5 | 20.5 | — |
| *colombianus* (1) | 185.0 | 95.0 | 33.0 | 23.0 | 23.5 | — |

[a] Means are shown with ranges in parentheses below each entry; coefficients of variation ranged from 2 to 6%.
[b] Middle toe measured from distal end of tarsus to base of nail.
[c] Weight in grams; sample sizes for body weights precede the range, all other sample sizes in parentheses following name of taxon; weights in quotes represent females with yolking eggs in oviduct.
[d] *Otus i. ingens* includes "*minimus*" and "*aequatorialis*," but not *venezuelanus*; represents all specimens from Colombia (except Cerro de Perijá), Peru, and Bolivia.

and wing. Tertials and wing coverts same pattern as back, but background color slightly paler brown, the wavy crossbars not as dark. Outer webs of remiges banded with alternating bars of pale Antique Brown (Color 37) and dark Raw Umber to blackish, each bar about 6 mm wide. Inner webs mostly dusky, broken by increasingly pronounced bars of pale Antique Brown along distal third, the final bar (11–13 mm) forming a broad pale tip finely mottled with dusky flecks. Tail banded brown and blackish (eight bands of each), the distal darker bands breaking up into indistinct mottling. Facial discs warm brown like back, most feathers finely barred blackish (4–5 bars on each feather), discs becoming blackish near rims. Superciliary area and interorbital tufts pale, warm buffy tipped with brownish mottling; facial tufts with long, dark brown rachises forming stiff bristles about bill. Entire underparts strongly and uniformly suffused with rich, warm buffy, closest to Cinnamon (Color 39). Feathers of throat and breast finely mottled with wavy bands of warm, dark brown; lower breast, belly, and flanks almost solid Cinnamon, but each feather with a conspicuous dark brown shaft streak and one to three thin, wavy transverse brown bars near the distal end. Belly and crissum solid Cinnamon. Tarsi feathered to within 5 mm of toes, Cinnamon faintly mottled brownish, distal feathering becoming sparse. Soft part colors in life: irides dark brown, bill pale grey-green, toes pale pinkish flesh.

MEASUREMENTS OF HOLOTYPE.—Wing chord 156.0 mm; central rectrices 87.0 mm; tarsus 26.5 mm; culmen, base to tip 21.5, anterior edge of nostril to tip 10.3 mm; weight 88 g.

SPECIMENS.—Peru: AMNH (holotype); FMNH 317314 (♂) from type locality, 2450 m; LSUMZ 87093 (♂), -94 (♀), -95 (♀), -96 (♂), from 12–20 km by trail east of La Peca, Dept. Amazonas, 1830–2030 m; LSUMZ 87097 (♀) from Playón, 2 km south of El Carmen on Río Samaniego, Dept. Piura, 1695 m. Ecuador: ANSP 176694 (♂) and -95 (♂), both from west slope of Cordillera del Cutucú, south of trail from Logroño to Yaupi, 2225 m. Colombia?: ANSP 2439 (unsexed), from "Bogota."

ETYMOLOGY.—We are pleased to name this species in honor of Roger Tory Peterson, in recognition of his many lasting contributions to field ornithology, conservation, and wildlife art, both to us personally and throughout the world.

## REMARKS

*Variation among paratypes.*—Nine specimens are available from four known localities. A tenth specimen, labelled "Bogota," recently was discovered by M. Robbins within a tray of unidentified *Otus* at ANSP. The otherwise typical body plumage of one male (FMNH 317314) includes numerous downy feathers that are paler and more heavily barred than on other specimens. Its testes were small (2 × 1 mm). Presumably this specimen was completing first prebasic body molt when collected. All other specimens appear to be in adult plumage. Sexual dimorphism, if present at all, is slight (Table 1).

As is typical in most *Otus,* substantial individual variation exists in details of adult plumage. Discrete color phases are less apparent than in many species, perhaps masked by the strong suffusion of cinnamon throughout all specimens. The specimens, however, do span a range from "brown" through "red" color types. The extremes are nearly as different from one another as the color phases in truly polymorphic screech-owls.

In *petersoni,* however, most specimens exhibit mosaics of intermediate characters. In the brownest extreme (the holotype), the dark shaft streaks on breast and belly are thin, fine lines transversed by numerous, well-defined brown cross-bars. On most other specimens, especially the reddish ones, these shaft streaks are broad and the crossbars are diffuse and less numerous. In the reddest specimen (ANSP 176694) the cross bars are mostly replaced by broad, diffuse patches of dark rufous, making the breast and upper belly almost solid rufous-brown. In this specimen, the crown, mantle, and inner remiges are dark rufous-brown, almost lacking any crossbars. In contrast, the brownest specimens are highly vermiculated dorsally and on the exposed edges of the remiges. Those specimens with the reddest facial discs lack the fine, dark facial barring of the browner specimens. In general, the obsolescence or loss of fine barring and dark vermiculations among the reddest specimens matches the pattern found among other, polymorphic *Otus* in which red phases occur (Marshall 1967).

Despite the variation from reddish to brownish, all ten specimens share the rich cinnamon undercoat, down, and background coloration. Except for a few small, whitish feather tips in the malar region of the reddest specimens (especially ANSP 176694), no specimen has any white on it whatsoever. In general, the intensity of the cinnamon-buff ground coloration is uniform across the underparts of each specimen, and it matches the color of the unbarred scapulars in each case. The darkest underparts belong to the reddest specimens, and the palest belong to a light reddish-brown male (LSUMZ 87093).

*Breeding and molt.*—All specimens were collected between 7 July and 16 August (in 1976, 1978, and 1984). The largest testes (those of the holotype) measured 7 × 4 mm on 17 July 1976. Those of the five other males varied from 1 × 2 mm to 4 × 4 mm. The ovaries of one female (LSUMZ 87097) collected 11 July 1978 appeared slightly enlarged, but no follicles exceeded 2 mm. We surmise that July and August, which are dry season months, are substantially past the annual breeding season of *O. petersoni.* This is supported by the existence of a first-year individual nearly in adult plumage on 28 July 1976, as mentioned above. Furthermore, light body molt was present on virtually all the specimens. One of the Ecuadorian specimens was replacing its innermost three pairs of rectrices, and the other had newly emerged ninth and tenth primaries (both specimens collected on 10 July 1984).

*Habitat and ecology.*—The habitat at the type locality is described in detail in Fitzpatrick et al. (1977, 1979). The Cordillera del Cóndor is an isolated ridge rising to about 2500 m, forming a border between Peru and Ecuador over most of its length. It is capped by subtropical forest, en-

shrouded by clouds over much of the day above 1900 m. The exposed, leached sandstone ridges harbor an unusually stunted forest that is poor in both bird and plant diversity (Fitzpatrick et al. 1977). The Cordillera del Cutucú, due north of the C. del Cóndor, is a northerly massif of the same line of isolated ridges. These two sister ridges are separated by a deep valley at the headwaters of the Rio Santiago. The habitat on the Cutucú at 2225 m was humid, mossy cloud forest (M. Robbins, T. Schulenberg, and F. Gill, pers. comm.). Southeast of the type locality, across the Río Marañon, lies another, even larger isolated massif east of Bagua (Cordillera Colán). In 1978 an LSUMZ party collected four specimens of *petersoni* between 1830 and 2030 m, also in cloud-forest.

An important additional specimen (LSUMZ 87097) was mist-netted "in second growth" at about 1695 m on the eastern slopes of the main Andes (Playón), approximately 50 km west of the type locality. This specimen indicates that *petersoni* is not entirely restricted to the isolated eastern ridges (Fig. 1), as certain other taxa in this region appear to be.

At two localities in Peru and the single locality in Ecuador (Fig. 1), the closely related *O. ingens* was collected along with *petersoni*. Overall, specimen records indicate that *ingens* occupies elevations slightly below those of *petersoni* (Fig. 2). Although they were collected at identical sites in three places, we suspect that *petersoni* generally occurs slightly higher on the mountain than does *ingens* where the two species are sympatric. In this respect, *petersoni* probably geographically replaces the newly described Cloud-forest Screech-Owl (*O. marshalli*), which occurs above *ingens* on eastern Andean massifs in the Peruvian departments of Pasco and Cuzco (Weske and Terborgh 1981, Schulenberg et al. 1984) (Fig. 1).

*Voice.*—On 23 July 1976 O'Neill recorded vocalizations of an unidentified screech-owl in the vicinity of the type locality, at 2200 m. These sounds are similar to a distant recording made by Schulenberg and Robbins on the Cordillera del Cutucú, uttered in response to playback by a male *petersoni* that was collected (ANSP 176694). O'Neill's excellent recording (Cornell Laboratory of Natural Sounds No. 18048) contains ten full, natural songs and several shorter phrases that apparently represent a second call type. All the songs are similar, consisting of a simple, long series of separate notes (range = 29–39, $\bar{x}$ = 34) delivered in rapid succession (0.15-sec intervals) sliding slightly up the scale about half a musical note, holding there for about 20 notes, then fading and sliding back to the original pitch. The entire phrase lasts 4.8–5.8 sec depending on the

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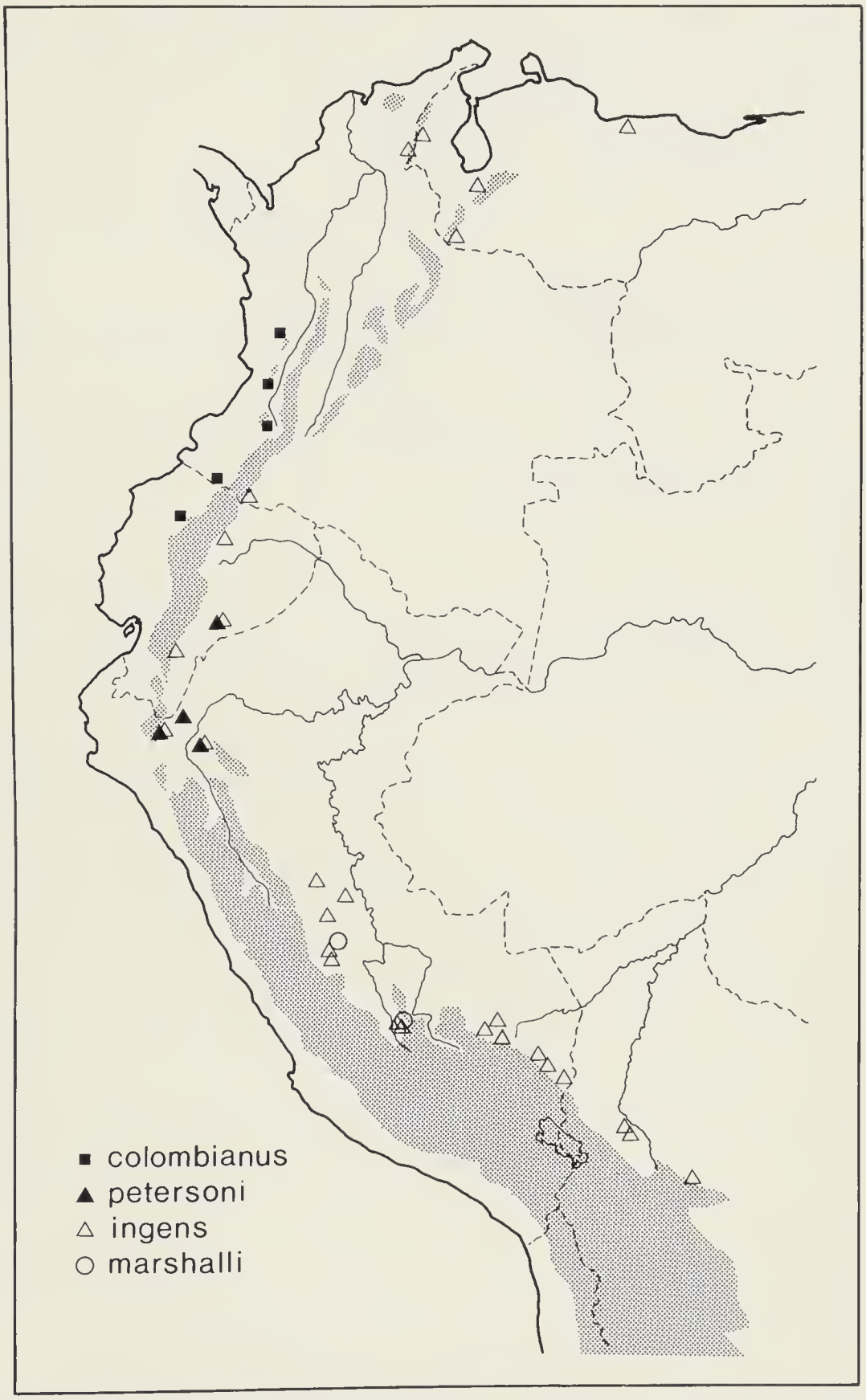
FIG. 1. Known distributions of four Andean species of *Otus* that possess dark-brown eyes. Individual localities are plotted for all specimens known to the authors (voice recordings




only for one locality of *ingens* in Venezuela). Stippling delineates area above 3000-m elevation.

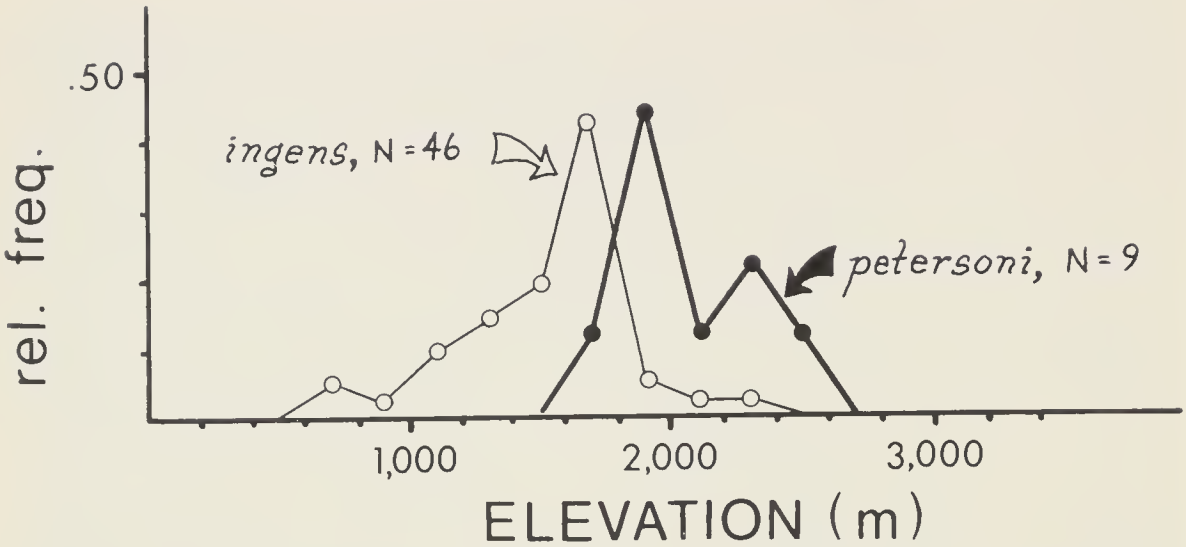



FIG. 2. Relative frequency of occurrence at different elevations (200-m intervals) for 46 specimens of *Otus ingens* and 9 specimens of *O. petersoni.*

number of notes uttered. No change in cadence occurs within the phrase. Volume increases gradually from quite faint introductory notes to a constant level at about the tenth note, in conjunction with the gradual, half-note increase in pitch. The pitch begins to descend at about note 27–30. The volume remains at its maximum for a few of these final notes, then fades off on the last two or three notes. Natural intervals between songs on O'Neill's recording range from 27 to 60 sec (mean = 44 sec). In Schulenberg's recording, the song is quieter, faster, and shorter than the one described above. It appears to be a "whisper-song," as the individual was at close range and was calling in response to playback of the second call type, described below (T. Schulenberg, pers. comm.).

The second call type consists of one to six notes that appear as inverted "U's" on the sonogram. These are longer notes than those in the primary song, each one an explosive whistle that rises and falls sharply. This note is uttered singly at several points on O'Neill's recording (perhaps by a second individual?). One time, a series of six such notes is uttered, about one note per sec, with the first and final ones softer than the middle four. A similar note appears in Schulenberg's recording of the Ecuadorian individual.

*Systematic relationships.*—The closest relatives of *petersoni* appear to be the other brown-eyed *Otus* of South America: *ingens, watsonii* (Tawny-bellied Screech Owl), and *marshalli.* As discussed below, the form described as *Otus ingens colombianus* by Traylor (1952) also belongs in this group, as a full species. Among New World *Otus,* the only other brown-eyed species is *flammeolus* of North and Middle America, a tiny species

whose systematic affinities within the genus remain unclear. The South American brown-eyed forms all have tawny-buff down and under-color, instead of whitish as in most members of the genus. They also have moderate to long ear tufts, and their primary songs—so far as known—consist of series of simple notes uttered nearly on a monotone and without sharp changes in cadence. (*O. ingens* has an alternate, shorter call that ends in a faster series.)

The following shared characters strongly suggest that the sister taxon to *petersoni* is *colombianus,* a form now known from ten specimens (plus a downy chick) and six localities in the western Andes of Colombia and Ecuador (Fig. 1). Iris color of *colombianus* also is brown (FMNH labels on 5 specimens; also Hilty 1977), confirming its membership in the brown-eyed assemblage. Based on the specimens at hand, *petersoni* and *colombianus* appear to be the only two taxa of Neotropical screech-owls to lack virtually any trace of white in the plumage. In both species, pale patches or bars—white in most other *Otus*—are solid cinnamon-buff. In the two brownest specimens of *colombianus* (including a long-misidentified specimen in the Paris Museum) the nuchal collar is nearly white, but all other pale areas remain tawny. Variation from reddish to brownish, as noted above for *petersoni,* is precisely replicated in *colombianus.* The rich tawny undercoat persists throughout both these series. Compared to *O. ingens* from east of the Andes, both *colombianus* and *petersoni* show substantially reduced transverse barring or vermiculations on the breast and belly feathers. The reddest specimens virtually lack this character altogether in *petersoni.* As described below, all other brown-eyed taxa show more ample tarsal feathering than do *colombianus* and *petersoni.*

In plumage pattern and color, *colombianus* and *petersoni* are so nearly alike as to suggest they could be conspecific. For the following reasons we suggest treating them as separate species, but we emphasize that based upon present data the question cannot be settled unequivocally. In linear measurements, *O. colombianus* is roughly 15 percent larger than *petersoni* (Table 1). Moreover, their proportions are not identical, with *colombianus* being relatively shorter-tailed and longer-legged than *petersoni.* As shown in Fig. 3, the ratio of these two characters is roughly similar within the brown-eyed assemblage, except for *colombianus.* Not only are the tarsi and feet of *colombianus* unusually long and robust for an *Otus,* but the tarsi are bare over much of their length and only sparsely feathered proximally (Fig. 4). This character is not present in any other South American *Otus* except *clarkii.* Indeed Hekstra (1982a, b) incorrectly proposed close affinities between *colombianus* and *clarkii* (yellow eyes, quite different plumage) based upon this character. While *petersoni* shows some reduction in tarsal feathering (Fig. 4), most specimens have at least a few sparse

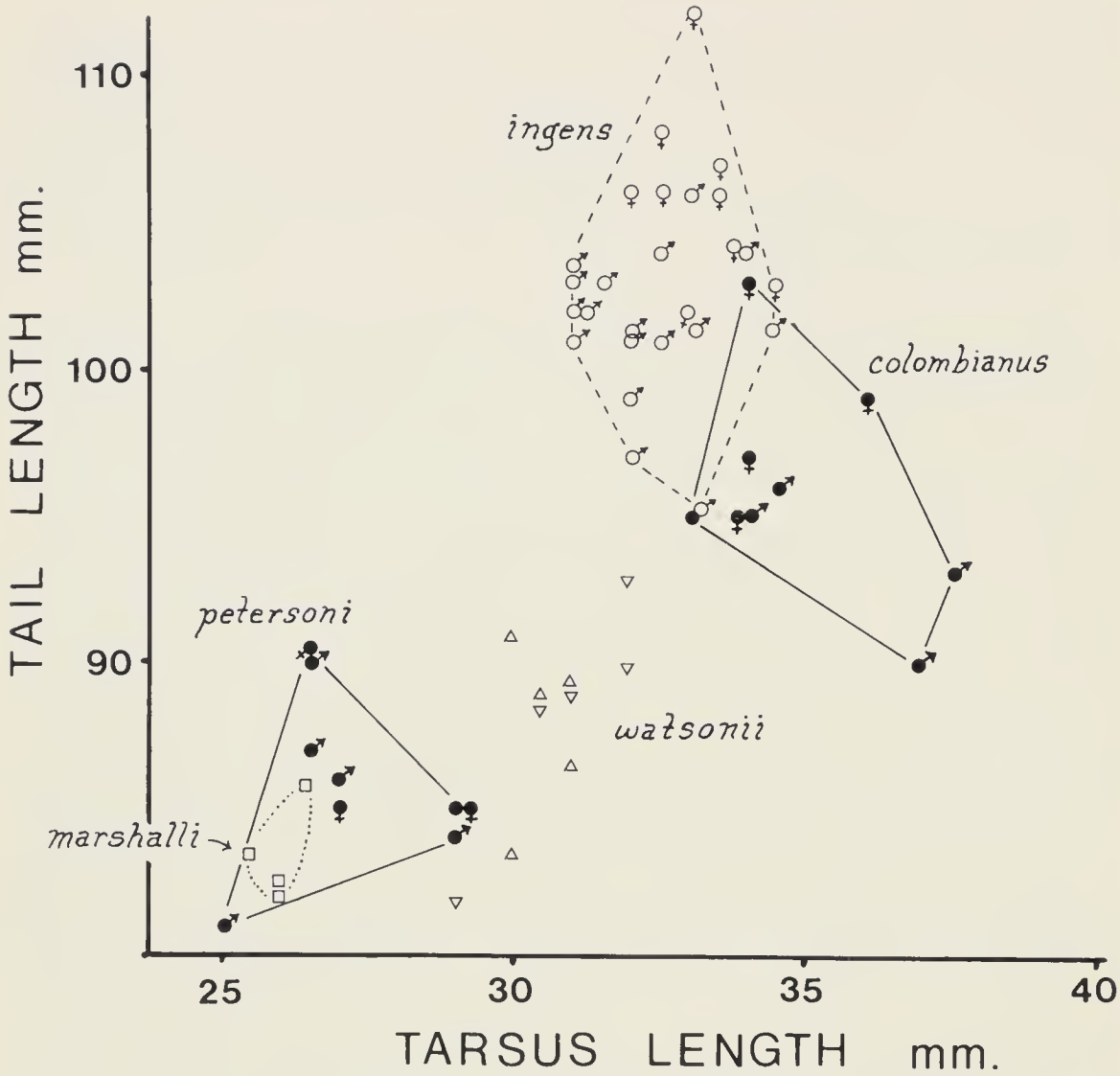



FIG. 3. Tail length plotted against tarsus length in five brown-eyed *Otus* of South America. Data are plotted for all available specimens of *petersoni, colombianus,* and *ingens.* Four males of *marshalli* and five of each sex of *watsonii* (upward-pointing triangles = males) are shown for comparison.

feathers all the way to the foot. Within the species group, this character state occurs as a graded series. Distally, the tarsus is totally bare in *colombianus,* sparsely feathered in *petersoni,* fully feathered in *ingens* and *marshalli,* and thickly, amply feathered to the foot in *watsonii* (Fig. 4). Finally, the plumages of *colombianus* and *petersoni* do show differences from one another in detail. In *colombianus* the ear tufts are slightly longer and more ample; the facial disc is less conspicuously edged blackish; and the underparts of all specimens show considerably more transverse barring, especially on the lower breast and belly, compared to *petersoni.*

In light of the above differences, our opinion is that *colombianus* and *petersoni* are best treated as two distinct members of a superspecies oc-

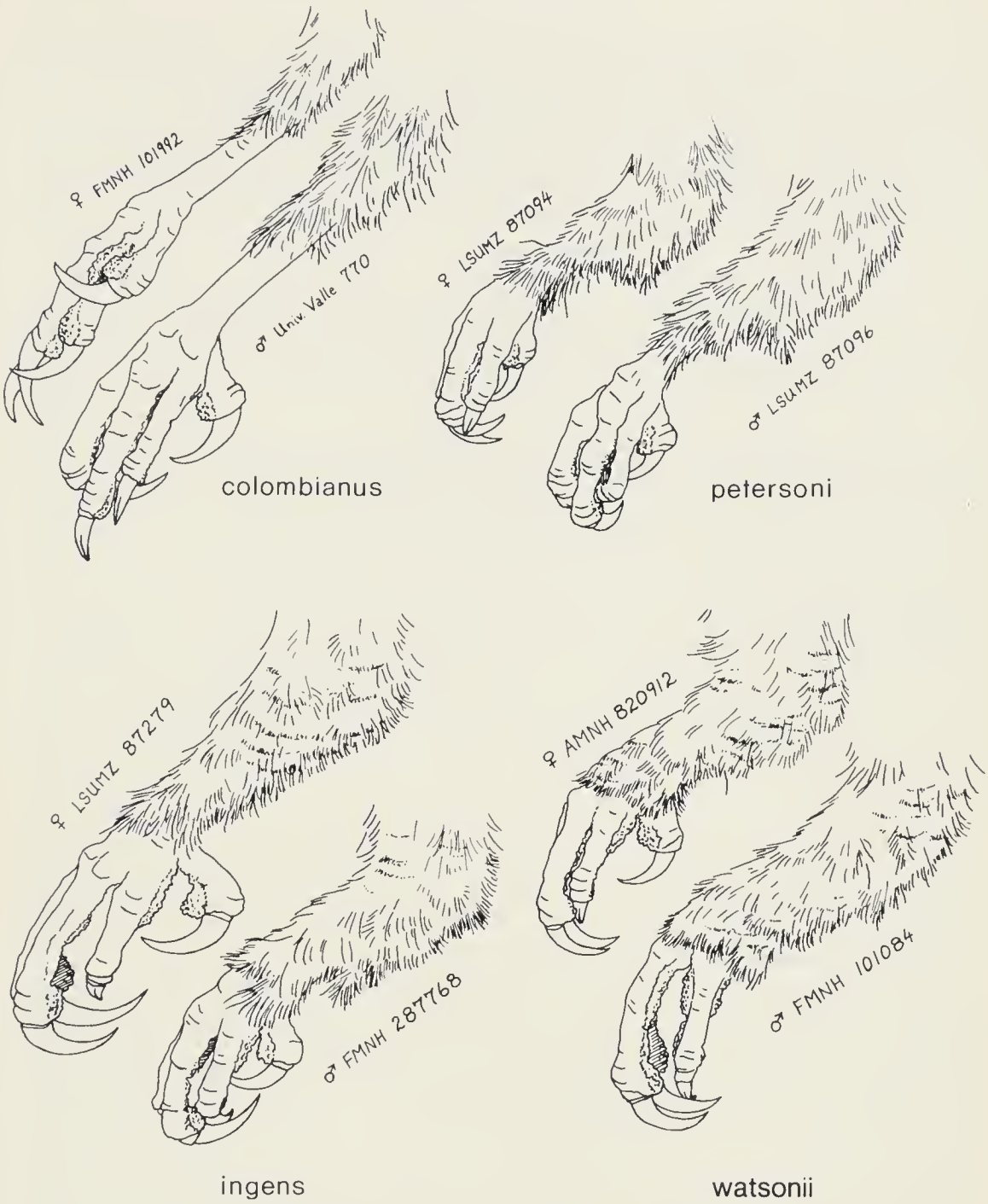



FIG. 4. Tarsi and feet of four brown-eyed *Otus* of South America, drawn from camera lucida. Female specimens are to the upper left in each pair. Museum catalog numbers are indicated for each specimen.

cupying the cloud-forests of the western and eastern Andes, respectively. The sister-relationships between these forms prove that both are specifically distinct from *ingens,* as *petersoni* is sympatric with *ingens.* We suggest that *O. colombianus* bear the English name Colombian Screech-Owl.

We have examined 36 of the 41 specimens of *O. ingens* of which we are aware; we assembled 30 of these, from all parts of the range, at the Field Museum. We concur with Bond (1951) and Traylor (1952) that *O. minimus* Carriker from the Andes of Bolivia is at best only barely distinct from nominate *ingens* of Peru and Ecuador, perhaps averaging paler and more finely vermiculated. Several specimens from central Peru match the Bolivian material at hand almost exactly. In addition, we find no characters that warrant continued recognition of the form *aequatorialis* described as a species by Chapman (1922; holotype examined). Adequate series of *Otus ingens* have accumulated only recently, and they indicate to us that the names "*minimus*" and "*aequatorialis*" were based upon individual variants within a highly variable but continuous population that runs from southern Colombia south to Bolivia (Fig. 1). The purported differences in size and plumage used by Hekstra (1982a) to distinguish *minimus* from nominate *ingens* are not apparent after controlling for sex and color phase. On the other hand, the smaller, paler *O. ingens venezuelanus* described by Phelps and Phelps (1954) warrants recognition. Recently, Fitzpatrick collected three additional specimens of *ingens* from the isolated coastal mountains north of Maracay, Venezuela (Pico Guacamayo, 1700 m; AMNH 824045, 824047, FMNH 317315). These represent a significant range extension of *ingens*. Whereas vocalizations of *ingens* are similar throughout the main Andes from Merida, Venezuela, south to Bolivia (personal observations, and recordings at Laboratory of Natural Sounds, Cornell University), the population atop the coastal mountains of Venezuela is vocally distinct, and may prove to be subspecifically separable even from *venezuelanus*.

Relationships among the dark-eyed *Otus* remain unclear to us, beyond the close affinities apparent between *petersoni* and *colombianus*. Despite differences in absolute size, proportions within the group are rather similar (e.g., Table 1). Although easily distinguished, certain reddish specimens of *O. watsonii* are astonishingly similar to *petersoni* and *colombianus*. Moreover, the primary song of *watsonii, north of the Amazon,* closely resembles that of *petersoni,* being slightly faster and longer. The song of southern *watsonii* consists of slow, low whistles, very different from its northerly populations, perhaps suggesting that two species are involved even within Amazonian *watsonii*. These observations raise the possibility that part or all of *watsonii* may be a lowland relative of *petersoni* and *colombianus,* with *ingens* and *marshalli* (and possibly *flammeolus*?) being more distant. Such conclusions are premature, however, until anatomical and vocal characters can be analyzed. Additional specimens and recordings are required, especially for *colombianus* and *marshalli,* before these phylogenetic analyses can be completed.

## SPECIMENS EXAMINED

*Otus petersoni:* type series, see above.
*O. colombianus:* Colombia: Cauca, El Tambo, "5000–7000 ft" (FMNH, 1 ♂, 3 ♀♀); Cauca, San Antonio, "7000 ft" (FMNH, 1 ♀); Choco, Cerro del Torra, 1860 m (UValle, 1 ♂); Valle, 9 km NNW Dagua, 1700 m (UValle, sex?); Valle, R. Anchicaya, 1300 m (AMNH, 1 ♀); Nariño, Ricaurte, Riserva La Planada 1700 m (Ris. La Planada, 1 ♂, color photos of specimen).
Ecuador: Nanegal (MNHP, 1 ♂).
*O. ingens:* Venezuela: Aragua, Pico Guacamayo, 1750 m (FMNH, 1 ♀; AMNH 1 ♂, 1 ♀); Cesar, above Eroca, "5500 ft" (USNM, 1 ♂).
Colombia: Nariño, El Carmen, "5000 ft" (FMNH, 2 ♂♂).
Ecuador: Río Sardinas (AMNH 1 ♂); Ambato, E of Los Baños (AMNH, type of "aequatorialis").
Peru: Cajamarca, Playón, "5500 ft" (LSUMZ, 1 ♀); Amazonas, 20 km E La Peca, "6450 ft" (LSUMZ, 1 ♀); Huánuco, Cerros del Sira, 2220 m (AMNH, 1 ♂); Huánuco, Cushi Libertad, 1800 m AMNH, 1 ♂, 1 ♀); Pasco, Conchapen Mtn., "5000 ft" (FMNH, 2 ♂♂, 1 ♀); Junín, Chanchamayo, 1200 m (FMNH, 1 ♂); Ayacucho, Huanhuachayo, 1660 m (LSUMZ, 3 ♂♂, 1 ♀); Cuzco, Cordillera Vilcabamba, 1350–1510 m (AMNH, 3 ♂♂); Cuzco, Consuelo, 1400 m (FMNH, 1 ♂); Cuzco, Quincemil, 1000 m (FMNH, 1 ♀); Ucayali, Abra Divisoria, "5000 ft" (LSUMZ, 1 ♂); Madre de Dios, Cerro de Pantiacolla, 980–1050 m (FMNH, 2 ♂♂, 2 ♀♀); Puno, Río Inambari, "2200 ft" (AMNH, 1 ♀); Puno, San José, Río Huari, "4200 ft" (LSUMZ, 1 ♂); Puno, Abra Maruncunca, 2000 m (LSUMZ, 1 ♂).
Bolivia: La Paz, Serranía Bellavista, 1350–1650 m (LSUMZ, 2 ♀♀).
*O. marshalli:* Peru: Cuzco, Cordillera Vilcabamba, 1920–2240 m (AMNH, 7 ♂♂, 1 ♀); Pasco, Santa Cruz, 9 km SSE Oxapampa, 2050 m (LSUMZ, 1 ♂).

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## COLOR PLATE

The Frontispiece painting of the Cinnamon Screech-Owl (*Otus petersoni*) has been made possible by an endowment established by George Miksch Sutton (1896–1982). The painting is by Roger Tory Peterson.

*Wilson Bull.*, 98(1), 1986, pp. 15–37

# MATING SYSTEM AND REPRODUCTIVE SUCCESS OF A SMALL POPULATION OF POLYGAMOUS SNOWY PLOVERS

JOHN S. WARRINER, JANE C. WARRINER, GARY W. PAGE, AND LYNNE E. STENZEL[1]

ABSTRACT.—This six-year study describes the breeding of a partly resident, partly migrant population of Snowy Plovers (*Charadrius alexandrinus*) in California. Migrants arrived between 6 January and 27 April, with females preceding males. Migrant males did not pair as early as resident males, whereas resident and migrant females paired at about the same time. Early pairbonds often were with the same mate in two consecutive years. Egg laying occurred from 23 March to 13 July. Replacement clutches were initiated between 11 April and 11 July, typically seven days after loss of the preceding one, and usually with the same mate. Over the season, the time required for a pair to complete the three-egg clutch decreased from five days to four days. During egg laying, males spent more time in the nesting territory and on the incomplete clutch than did females. Incubation averaged 28.4 days early in the season, but only 26.9 days late in the season. During daytime, males averaged only 10.7% of the incubation time, but they appeared to be the main incubators at night. Over six years, 58.2% of 189 clutches hatched at least one chick. Females normally deserted hatched young within six days; males attended the young for 29 to 47 days. Fledging typically occurred at about 31 days of age. Over six years, 39% to 42% of 296 chicks fledged. After deserting broods, at least 22 of 60 females renested with new mates. At least 10 of 18 males fledging chicks before 1 July renested with new mates, and in at least 13 of 27 cases, males losing broods before 1 July renested, usually with new mates. Males appeared to outnumber females by 1.4:1. Sexual differences in survival rates are nearly sufficient to account for the difference in sex ratio. We suggest that the female's serial polyandry may be a facultative response to a skewed sex ratio. *Received 12 Mar. 1985, accepted 19 Sept. 1985.*

Despite the proliferation of shorebird literature during the past 20 years, information on breeding success and mating systems of several shorebird species is lacking (Johnsgard 1981). This deficiency encumbers attempts to understand the evolution of shorebird mating systems, a topic of considerable recent interest (Pitelka et al. 1974, Graul et al. 1977, Oring 1982, Erckmann 1983, Lenington 1984). This paper addresses that lack of information for the Snowy Plover (*Charadrius alexandrinus*). We trace events during the breeding cycle from the acquisition of mates and nesting territories to the fledging of the last chick of a partly migratory, partly resident Snowy Plover population. We quantify nesting success and describe a polygamous breeding system in a species previously reported as monogamous (Rittinghaus 1956, 1975; Palmer 1967; Boyd 1972; Johnsgard 1981; Cramp and Simmons 1983; for an exception see Lessells 1984).

[1] Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, California 94970.

*C. alexandrinus,* a cosmopolitan species of temperate and tropical regions, comprises up to 13 subspecies, depending on the authority (Johnsgard 1981). Two subspecies are recognized for North America: *C. a. nivosus* west of the Rocky Mountains, and *C. a. tenuirostris* along the Gulf of Mexico, in the West Indies, and on islands off Venezuela (AOU 1957, Johnsgard 1981). Although breeding birds in Kansas, Oklahoma, and Colorado are reported to be *nivosus* (AOU 1957), some workers suspect they may be *tenuirostris* (J. Strauch, pers. comm.; R. Boyd, in litt.; Johnsgard 1981). In general, the species breeds along sandy coastal shores and on inland flats of high salinity or alkalinity (Cramp and Simmons 1983).

Knowledge of the breeding biology of *C. alexandrinus* is based chiefly on Rittinghaus's (1956, 1961, 1975) studies of the Kentish Plover (*C. a. alexandrinus*) and, for the North American subspecies, on Boyd's (1972) study of Snowy Plovers at Cheyenne Bottoms, Kansas. Both authors describe *C. alexandrinus* as monogamous, leading to a similar characterization in more general works (Palmer 1967, Johnsgard 1981, Cramp and Simmons 1983). Recently, Lessells (1984) documented polygamy in Kentish Plovers in southern France. We describe another polygamous breeding population of *C. alexandrinus* in California and provide details of its biology for comparison with Rittinghaus's and Boyd's studies.

## STUDY AREA AND METHODS

We studied Snowy Plovers from 1977 to 1982 on the central California coast at the Pajaro River Mouth on Monterey Bay, and from 1978 to 1982 in the California interior at Mono Lake.

*Pajaro River.*—At the mouth of the Pajaro River, plovers nested on sand spits and on a salt pan (0.8 km from the spits). The pan, which was situated between a beach front development and the edge of a tidal slough, consisted of three flat, barren patches of saline mud surrounded by salt marsh (primarily *Salicornia virginica* and *Distichlis spicata*). The plovers used an area 300 × 125 m, which was little disturbed by people. After 1977, the potential breeding habitat at the south end of the salt pan expanded when some of the salt marsh was bulldozed and denuded of vegetation as part of a slough enhancement project. By 1982, enough vegetation had invaded the bulldozed area to deter nesting plovers. Suitable nesting habitat on the spits included barren to sparsely vegetated areas above the high tide line. Dimensions of the spits on both sides of the river varied yearly between 100 m and 200 m in width and 400 m and 900 m in length due to winter storm erosion and shifting of the river mouth position. Human use of the spits was high relative to that of the salt pan.

At the salt pan during the breeding seasons of 1977 to 1979, we observed birds daily from a parked car, found most nests before first eggs, and checked nests several times a day at egg-laying and hatching times. From 1977 to 1982 we searched daily for nests, broods, and banded adults on the north and, after 1977, the south spits of the Pajaro River. During the six years there were only six broods for which no nest was found.

We color banded chicks and, after 1977, adults. Chicks were distinctively color banded

at the nest, by brood in 1977 and 1978, and by individual thereafter. We trapped adults with noose-covered wire mats placed in lines near plover flocks or around nests. The nooses snared the birds' legs as they ran over the mats.

The parental roles of the sexes were examined through the surveillance of birds at the salt pan in 1978 and 1979. One or two observers followed one to four pairs of plovers and recorded the time each bird spent in the territory and on eggs. There were 142.7 h of territory observation during the egg-laying period, 412.0 h during the incubation period, and 32.9 h during the hatching period. The average times each sex spent in the territory and on the nest were calculated by giving equal weight to observation time during each 3-h interval from 05:00 to 20:00 PST for the egg-laying period, to each h during the hatching period, and to each 3-h by 3-day period during the incubation period. Birds were easily sexed throughout the study through a combination of distinctive plumage (see Prater et al. 1977), observed copulations for many pairs, and, after 1977, individually color-banded birds.

During the breeding season we searched other Monterey Bay breeding sites for marked birds that had nested previously at Pajaro. Moss Landing salt evaporation ponds are 6 km south of the Pajaro River in Monterey County. Depending on water levels, up to 100 ha of dike margins and salt flats were available for nesting and feeding. One or more observers visited the Moss Landing evaporation ponds during each breeding season from 6 to 36 times between 1978 and 1982. Wilder Ranch State Beach, Santa Cruz County, is a 0.5-km long pocket beach between cliffs at the mouth of Wilder Creek, 27 km northwest of the Pajaro River. It was surveyed 6–17 times during the 1978 and 1979 breeding seasons, and from 1980 onwards, 3–5 times every week.

We checked for color-banded Snowy Plovers at the Pajaro River during each nonbreeding season beginning in 1978. Each year this coverage ranged from 47% to 82% of the days between October and March. Six days was the longest period between counts; single days made up 56% to 82% of the days missed. During the censuses we recorded which birds associated with one another both in and apart from flocks in an effort to detect the formation of pair bonds.

We organized volunteers to survey other sites along the coast and in the southern deserts of California to ascertain the whereabouts of individually banded plovers during the nonbreeding season. Observers made 881 to 1057 surveys at 83 to 150 sites each September to March period between 1979–80 and 1981–82.

*Mono Lake.*—Mono Lake, an elliptical 20 × 15 km alkaline lake, lies at the eastern base of the Sierra Nevada in Mono County. Snowy Plovers nested on old sand and pebble shoreline ridges and on alkaline flats that were exposed recently when the lake's water level declined. Our study site at Mono Lake consisted of approximately 10 $km^2$ of gently sloped, barren to sparsely vegetated lakeshore as described in Page et al. (1983).

We studied breeding Snowy Plovers at Mono Lake to supplement our work at the Pajaro River. Because the plover population there is large (Page and Stenzel 1981), we selected it over Pajaro for measuring the sex ratio of the breeding population. We banded 129 adults at their nests using the trapping and marking methods described for the Pajaro adults.

In both 1981 and 1982, 10 censuses of Snowy Plovers were taken between 1 and 19 June along 4.5 km of seeps that bordered an old lakeshore ridge and along 4.5 km of corresponding current lakeshore. One person walked along the seeps, and another walked as close to the lakeshore as possible. Each counted all Snowy Plovers seen and recorded their age, sex, whether banded, color combination, and the time and specific locations of the sightings. To test field accuracy in sex determination, two primary observers viewed 30 museum specimens in breeding plumage from a distance of 15 m with 9 × 35 binoculars. One observer's determinations matched the museum labels 93% of the time, the other's matched the labels 100%.

Because of the 2-km width of the study area, we accounted for less than 100% of the plovers. Therefore, in the analysis of census data, we used a standard capture-recapture technique of estimating population size (Seber 1982) modified as described below to compensate for differences between recapturing and resighting as methods of detecting individuals. Because we observed a few marked plovers between censuses or found them in the study area on nests which we knew to be active during the census period, we were able to supplement our knowledge of which marked plovers were present in the study area during each census. Additionally, as marked individuals may be seen more than once on a census, we used multiple sightings of marked birds to estimate the overcounting of all birds due to movements of individuals. In the calculations for each year, we considered only birds marked in previous years, so that the nesting stages of marked birds represented those of all plovers. Population size estimates were made for each sex and year separately. The equality of corrected totals for each sex on each census was compared using Wilcoxon's matched-pairs signed-ranks test for each year.

## RESULTS

Snowy Plovers occurred year-round at Pajaro, but not all birds were residents. From 1978 through 1982, 40.9% of 44 marked males and 23.7% of 59 marked females that nested also occurred regularly between October and March (residents). Another 43.2% of the males and 42.4% of the females bred at Pajaro but were absent from November to at least January (migrant breeders). During the same period at least 18 marked males and 16 marked females wintered at Pajaro (occurred regularly from at least November to February) and bred elsewhere (wintering birds). Other birds followed inconsistent patterns or disappeared too quickly to be categorized. Three males and six females changed patterns between years: one male, a resident the first year, appeared briefly in the second and third years, and became a migrant breeder in the fourth and fifth years; two males and three females that were migrant breeders and two resident females abandoned Pajaro as a breeding site, yet were known to be alive; and a sixth female was resident for four years, except for the third breeding season, when she was absent. The situation at Pajaro differs from the interior of western North America where most, if not all, breeders migrate to coastal wintering areas (unpubl. data).

*Arrival of migrant breeders.*—Female migrant breeders arrived at Pajaro as early as, if not earlier than, migrant male breeders (Fig. 1). Although the arrival dates of both sexes spanned about the same period, the overall mean arrival dates were 9 March for females and 24 March for males, a difference that was marginally significant (Mann-Whitney $U$-test, $P = 0.0586$).

*Pairbonds.*—We were unable to determine when and how pairbonds formed, but on numerous occasions we saw behavior that we believed led to pair formation. Such behavior was typified by a male repeatedly calling *turwheit* from a territory that he had defended against other male

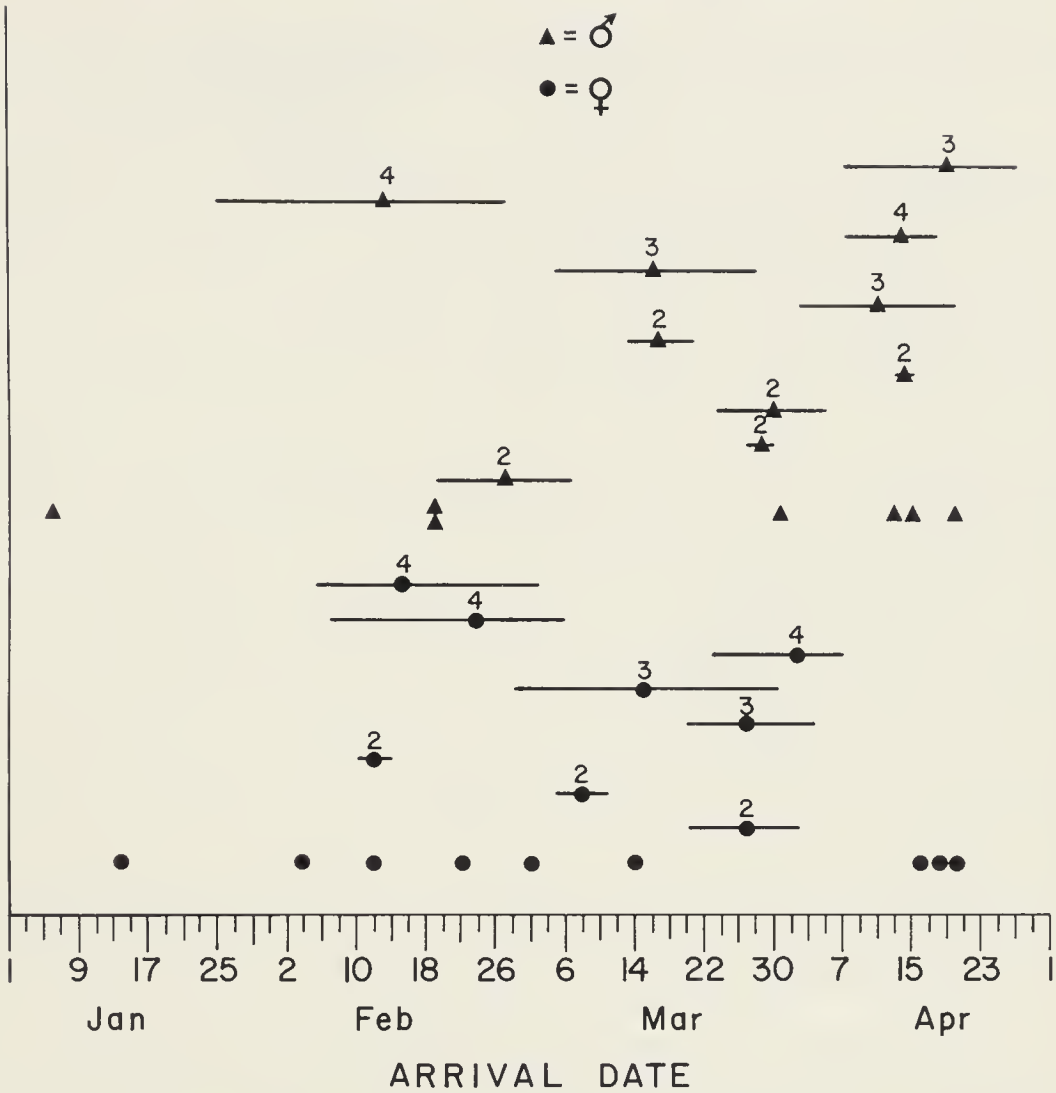


FIG. 1. Arrival dates of marked Pajaro Snowy Plovers. Horizontal lines give the ranges, circles or triangles the means, and numbers the sample sizes of years for individuals. Single dates for individuals are shown as circles or triangles without sample sizes.

plovers. When a female arrived, the male adopted a posture in which bill, body, and tail were parallel to the ground, the head was extended, and the throat feathers were puffed out as the bird moved about, almost gliding. The male approached and passed the female in this posture and then began scraping by lowering his breast to the ground and kicking backward alternately with his feet, gradually rotating his body. Usually, scraping occurred where the bird had scraped before so that there was a depression in the ground. Sometimes the female squatted in the depression and rotated slightly; although this occasionally led to copulation, the sequence usually was repeated at several scrapes before the first copulation occurred. Sometimes the female flew off or was driven off by the male, and no copulation occurred. Early in the season, however, birds that eventually

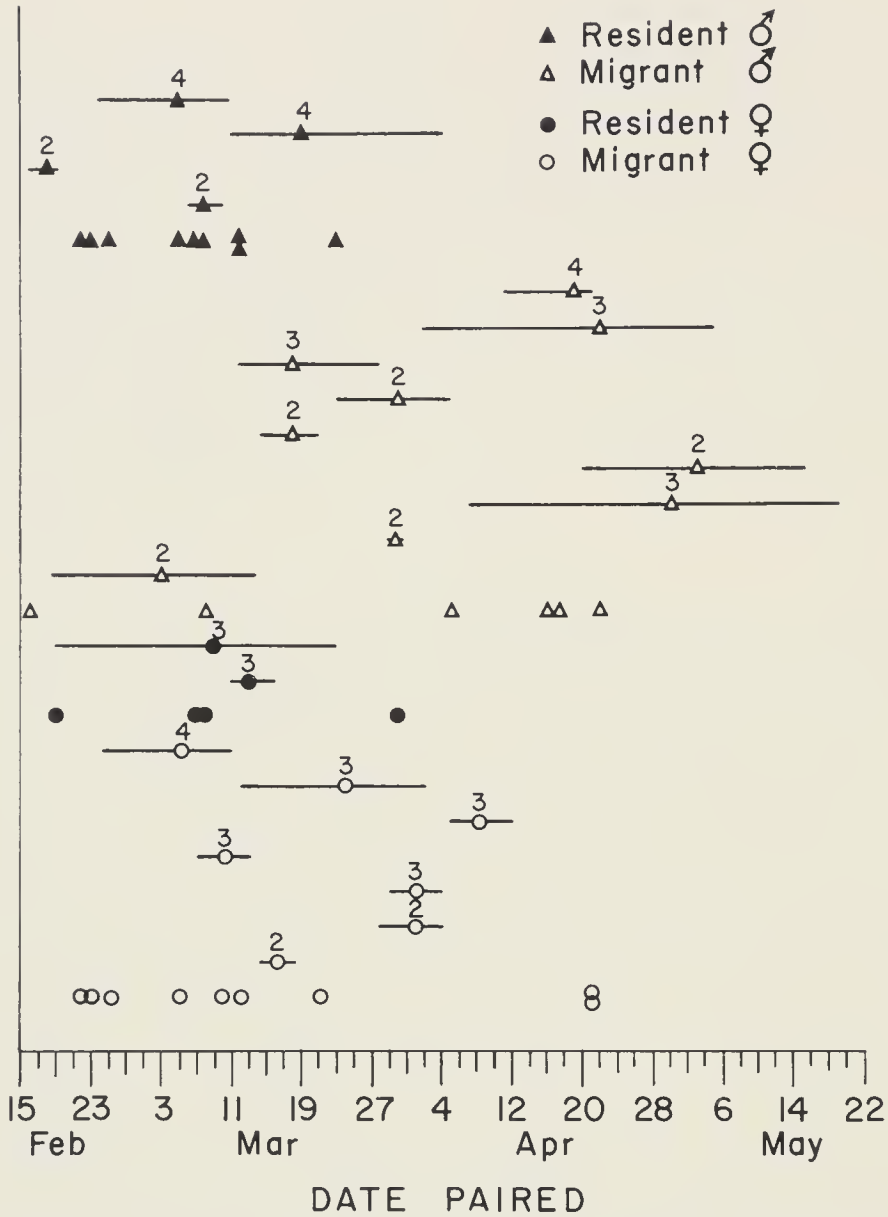


FIG. 2. Dates by which resident and migrant breeding Snowy Plovers were paired at Pajaro. For symbols see Fig. 1.

nested together were consistently beside each other within and apart from roosting flocks day after day, and we saw no scrapes or scraping activity. This suggests that pairbonds can be established before scraping occurs. We use the first date that eventual nesters were seen associating with each other to estimate the time of pair bond formation.

Early season pair bonds formed between residents (7 cases), migrant males and females (15 cases), migrant males and resident females (10 cases), and migrant females and resident males (11 cases). Mean estimated pairing dates were 10 March for resident females, 19 March for migrant females, 6 March for resident males, and 3 April for migrant males (Fig.

2). Residents were paired significantly earlier than migrant breeders for males (normal approximation for Mann-Whitney *U*-test, $P = 0.001$) but not for females ($P = 0.3$).

An individual's earliest nesting attempts were with the previous year's first partner on 13 of 29 possible occasions. In 5 of the 16 remaining cases, one adult appeared to be paired before the other arrived, but in 11 instances new mates were chosen, despite the apparent availability of the former mate. Kentish Plovers also pair with a previous year's mate, although a partner change from one year to the next is described as the rule (Rittinghaus 1956, 1961).

*Territories.*—Snowy Plovers posture, chase, and fight when defending territories. Territory sizes were always less than 0.5 ha at the salt pan, where boundaries on two to four sides were defined by the interface of barren flat with salt marsh vegetation. Beach territories may have been larger, but we lacked sufficient observations to determine their size.

A nesting territory was not a prerequisite for pair formation. Despite daily coverage at the salt pan, in only 14 of 47 cases did we find unpaired territorial males. The remaining males were paired when first seen on territories. Neither is a territory necessary for pairbond formation in Kentish Plovers (Rittinghaus 1961, 1975). When advertising, unpaired, standing Pajaro males called *turwheit* repeatedly from their territory. We did not see aerial advertisement such as the bat-like song flight Rittinghaus (1975) describes as rare, or the unsteady, tern-like flight Dement'ev and Gladkov (1969) mention for the Kentish Plover.

It was not always possible for Pajaro birds to occupy the same territory in consecutive years because of beach erosion during the winter. In the 21 possible cases where males and females could occupy the same territory and remate with each other two years in a row, males used the same territory in 15, and females in 9, instances. When pairing was with a previous year's mate, the pair used the previous year's territory in 7 instances and a different territory in 3 instances. When birds changed mates between years, males changed territories in only 3 of 11 cases and females in 9 of 11 cases. These results were consistent with those of Rittinghaus (1956, 1961) who reports that when Kentish Plovers change partners from one year to the next, it is usually the male that goes to the previous year's territory.

Snowy Plovers did not always retain a territory for renesting attempts after failure. After clutch failure induced by human or natural causes other than predation, pairs with at least one banded bird renested in the same territory in 12 of 23 instances. Pairs retained a territory in only 1 of 11 instances when a predator destroyed the clutch. Eight departing pairs moved 200–800 m to new Pajaro territories, one moved 4 km to a new

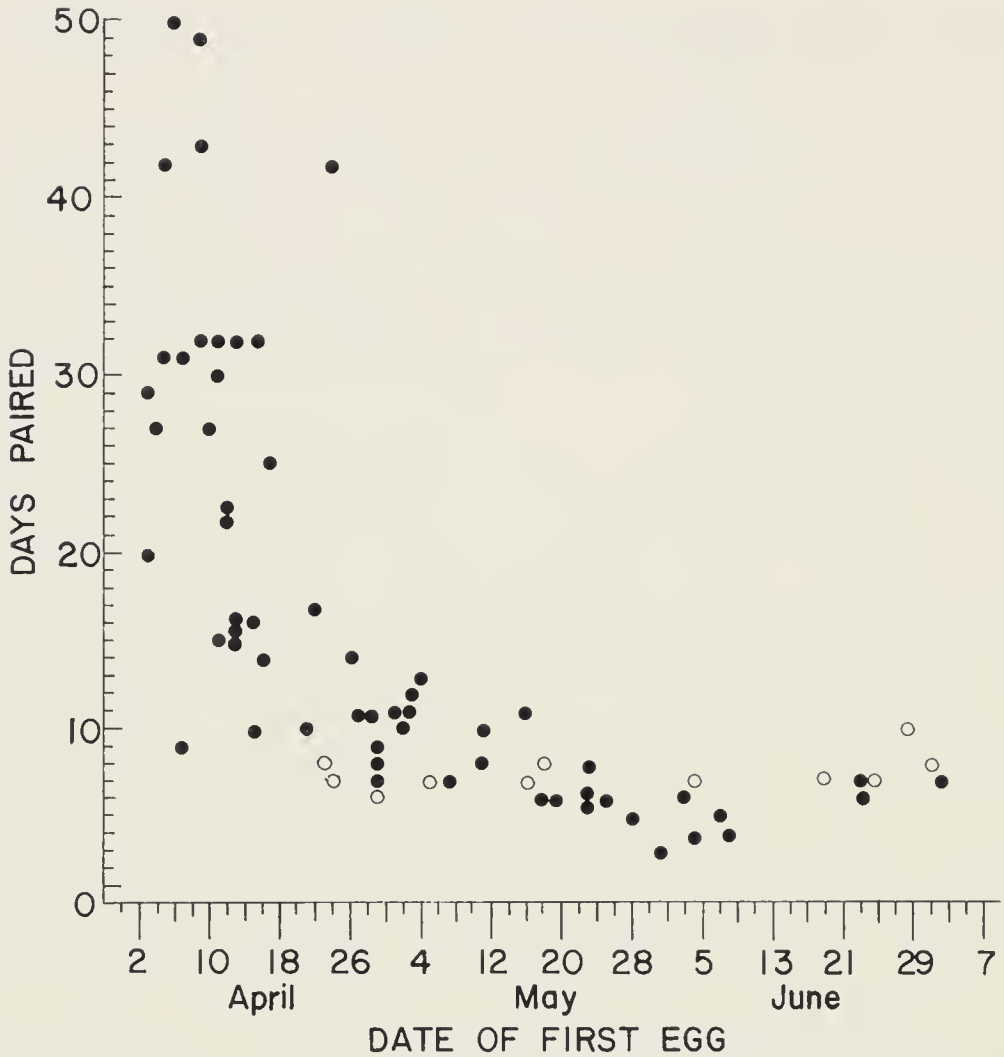


FIG. 3. Closed circles show the number of days paired before the first egg was laid. Open circles show the time between clutch failure and the first egg of renesting attempts of established pairs.

beach territory, 11 moved 6 km to the Moss Landing evaporation ponds, and one pair disappeared.

*Egg laying.*—Egg laying spanned 16 weeks at Pajaro with the earliest egg on 23 March and the latest egg about 13 July. Every year except 1982, egg laying began by late March and lasted to at least 29 June. Overall, at least 6 clutches were begun in March, 84 in April, 62 in May, 32 in June, and 6 in July. At least 10 of the April clutches, 8 from May, 9 from June, and 2 from July were renests after failure. At least 5 from May, 10 from June, and 1 from July were renests of females after the successful hatching of a previous clutch.

The clutch sizes in completed Snowy Plover nests at Pajaro were 1 with four eggs, 160 with three eggs and 10 with two eggs. Three of the two-egg clutches were discovered after incubation had begun and might have held a third egg at one time. Larger clutches are possible. Page, Peaslee,

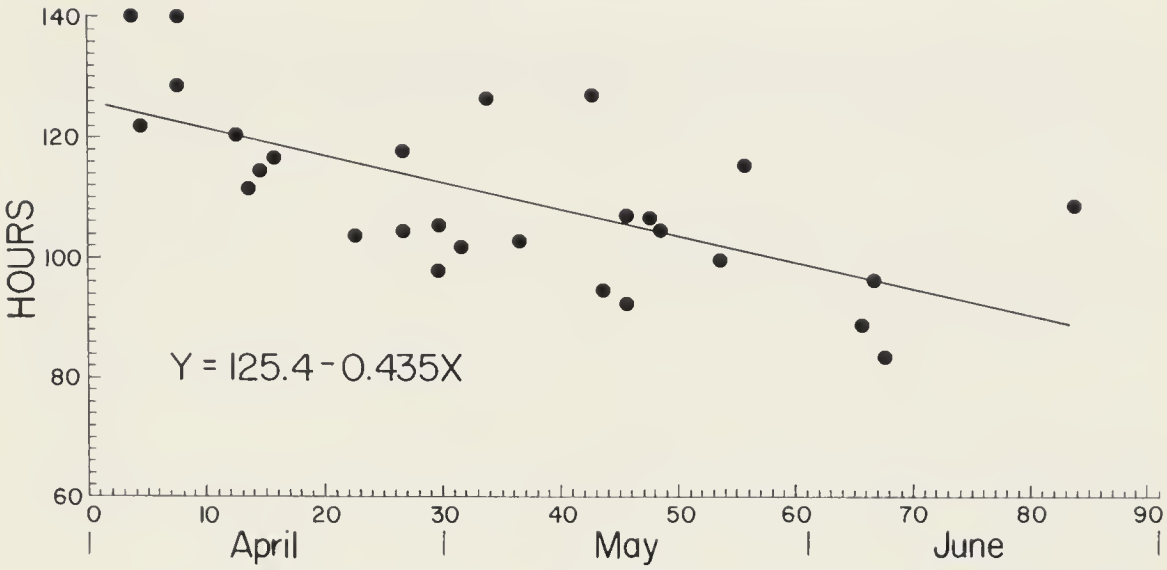


FIG. 4. Seasonal variation in the hours elapsing between the laying of the first and last of the three eggs in Snowy Plover clutches at Pajaro. The slope of the regression line is significantly different from 0 ($P = .00016$).

and Widrig (unpubl. data) found one clutch with five eggs and two with six in 1977 at Big Lagoon, Humboldt County, California. One female-plumaged bird sat on one of these nests readily when the observers were near, but she was aggressively displaced by another female on two occasions when the observers retreated. This suggested that two females laid the eggs. Cramp and Simmons (1983) mention a similar situation in the Kentish Plover, where a male and two females attended a single nest with five eggs.

At Pajaro, the interval from pairbond formation to the first egg ranged from 50 to 3 days and decreased during the breeding season (Fig. 3). Copulations, which are well-described in Rittinghaus (1956) and Boyd (1972), occurred from 25 days before to 3 days after the first egg was laid. At the salt pan, 89% of 172 observed copulations were prior to the first egg and none was after the second. By contrast, Piping Plovers (*C. melodus*) copulate throughout the egg-laying period (Cairns 1982), and Killdeers (*C. vociferus*) copulate throughout the incubation period (Bunni 1959).

During the egg-laying period, Snowy Plovers were often absent from their salt-pan territories. In the 10 territories, males were absent 37.7% (SE = 7.6%) and females 52.6% (SE = 5.6%) of the time during the day; in 9 of the 10 territories males were absent during less time than females (randomization test for matched pairs, $P = 0.0078$). The 10 males averaged 16.6% (SE = 3.0%) and the 10 females 10.3% (SE = 2.7%) of the time during the day on the eggs. In 7 of the 10 cases, males spent more time on the eggs than females ($P = 0.0186$).

We know the time at which 58 eggs were laid. Two to seven were within each hour interval between 06:01 and 19:00, indicating laying occurs at any time during daylight. The daytime (06:01–18:00) to nighttime ratios for eggs were 20:3 for egg one, 22:17 for egg two, and 23:6 for egg three. The difference is significant ($\chi^2 = 7.91$, $P < 0.02$), indicating that egg two was more likely to be laid after dark than eggs one or three. The usual time between consecutive eggs ranged from 46.5 to 77.5 h and averaged 61.6 h (SE = 4.2, N = 8) between eggs one and two, and 55.4 h (SE = 2.2, N = 17) between eggs two and three, a difference that was not significant ($t$-test, $P > 0.05$). Rittinghaus (1956) reports 18–72 h between Kentish Plover eggs, but that 48 h is normal. The time required to complete Pajaro clutches decreased from an average of about five days for early nests, to about four days for late ones (Fig. 4).

*Incubation.*—Snowy Plovers typically began sustained incubation when the last egg of the clutch was laid. Incubating plovers were found as early as 29 March and as late as 9 August at Pajaro, and during the six years were always present at least from 2 April to 4 July. Incubation from the last egg laid to the last young hatched ranged from 26 days to 32 days ($\bar{x} = 27.4 \pm 0.2$ [SE]) with the earlier nests averaging longer periods than later ones ($\bar{x} = 28.4 \pm 0.3$ for 19 nests started before 8 May; $\bar{x} = 26.9 \pm 0.1$ for 38 nests begun later; $t$-test, $P < 0.01$). The same trend was observed at Mono Lake where incubation periods ranged from 25 days to 32 days, but averaged 28.8 days in four nests started before 1 June and only 25.4 days for five later ones. Even the late season Pajaro incubation periods were longer than Boyd (1972) gives for Cheyenne Bottoms, Kansas, where eight clutches hatched within 24 to 26 days ($\bar{x} = 25.5$ days). Rittinghaus (1975) gives a range of 23–29 days and a mean of 26.3 days (N = 43) for incubation in the Kentish Plover.

During daytime, male Snowy Plovers spent less time incubating than females until hatching began. In eight salt-pan territories, males were absent 84.1% (SE = 3.1%) and females 11.2% (SE = 1.7%) of the time during the day. Males incubated an average of 9.5% (SE = 3.3%) and females 79.7% (SE = 3.4%) of the time during the day. In all territories, males spent less time incubating than females. Our results concur with those of others who reported that in *C. alexandrinus* females take the bulk of the daytime incubation duty (Boyd 1972, Rittinghaus 1975, Nakazawa 1979, Cramp and Simmons 1983).

We know less about nighttime incubation, but we suspect that males incubate at night. We found males incubating in 90.4% of 73 dusk nest checks. This differed from the daytime, when males averaged 10.7% (SE = 2.0%) of the incubation time on the eight salt-pan territories. At Mono Lake, Page and Stroup (unpubl. data) found only the male incubating a

clutch when they photographed a nest one night using a flash every 45 min from 23:00 to dawn. Boyd (1972) reported that the female Snowy Plovers incubate at night, and Rittinghaus (1975) reported that male Kentish Plovers incubate from late afternoon or early evening to the early morning hours.

*Clutch Failures.*—During the study, we found 187 nests and 6 broods at Pajaro. Our banding caused failure at four nests, which are excluded from all calculations of productivity. The six broods are included for a total of 189 nests.

Desertion caused failure at four nests; three additional desertions that occurred after the study supplement our information. In seven cases where one sex (two males and five females) deserted during the first 16 days of incubation, the other sex eventually also abandoned the clutch, whereas in two cases (one male and one female) where abandonment occurred between the eighteenth and twenty-second day of incubation, the remaining parent hatched the clutch. Lessells (1983) reports that single-parent Kentish Plovers also hatched clutches deserted by the other parent during the later period of incubation. In addition, Lessells (1983) found female Kentish Plovers were more likely to desert than males.

Both parents sometimes deserted Pajaro clutches that were reduced to one egg, and these desertions also appeared related to length of incubation. Parents abandoned four clutches reduced to single eggs at between 3 and 13 days of incubation, but not two clutches reduced to one egg on the twenty-sixth and thirtieth days. After this study, two other clutches reduced to single eggs, one between the twelfth and eighteenth day, and the other between the eighteenth and twenty-fourth day, were not deserted, and both hatched. We classified clutches reduced to one egg and then deserted as "destroyed."

Seventy-five of 189 nests at Pajaro were destroyed by causes other than desertion. People destroyed 26 nests, all but one of them on the beach, by driving over them, stepping on them, or by taking the eggs. All wind losses (N = 12) and losses of unknown cause (N = 4) were on the beach. Seventy-five percent of the clutches lost to wind, and all lost to unknown causes, disappeared on weekends and holidays, although these days made up only 30% of the time nests were in existence. As most human use of beaches occurred on holidays and weekends, we believe people indirectly or directly caused many losses we attributed to wind or unknown factors. People may have kept incubating birds off nests during strong winds, allowing eggs to be scattered or buried.

Predators destroyed 19 Pajaro nests; at least one was taken by an American Crow (*Corvus brachyrhynchos*), 6 by unidentified gulls (*Larus* spp.), and the remainder by various mammals. Gulls did not actively seek

clutches, but destroyed them when individuals in roosting flocks trampled on or accidentally discovered the eggs and ate them. At Mono Lake, gull predation is deliberate, and many clutches are taken (Page et al. 1983).

High tides caused destruction in nine instances, rain caused destruction in three, and the embryos inexplicably died in two. We identified no other causes of clutch loss at Pajaro.

*Renesting after clutch failure.*—Snowy Plovers typically renested after clutch loss until July. Renesting occurred between 11 April and 11 July. In 12 of 13 accurately determined instances, six to eight ($\bar{x}$ = 7.1, SE = 0.2) days elapsed between clutch destruction and subsequent clutch starts; in the thirteenth instance, 14 days elapsed. In five additional cases a new clutch was begun in two to four days after the destruction of a partially completed one, resulting in a second clutch of three eggs. Pairs renested up to five times. Rittinghaus (1975) reports that Kentish Plovers renest readily after clutch destruction, in as few as four to five days after loss of the first. Renesting from 5 to 14 days after clutch failure in other *Charadrius* plovers is not uncommon (Bunni 1959, Graul 1975, Cairns 1977, Bergstrom 1982).

Snowy Plovers remained paired in 26 of 30 cases involving renesting of banded pairs at Pajaro. One female chased off the female of a pair attempting to renest, and the aggressive female nested with the male whose mate she had driven off; otherwise we could not account for the reasons that pair bonds dissolved. Lessells (1984) reported that Kentish Plover pairs remained together in 11 out of 13 instances after clutch failure, and Rittinghaus (1975) reported that Kentish Plover partner changes after clutch loss are rare.

*Hatching.*—Eggs hatched during any time of the day and at night. From 1 to 33 h elapsed from the emergence of the first to the third young in 28 three-egg clutches; 43% hatched in less than 6 h. During hatching, males were present in nine territories an average of 72.3% (SE = 7.6%); females were present 87.5% (SE = 4.7%) of the time. Males spent 39.0% (SE = 5.3%) and females 54.0% (SE = 5.0%) of the time on the nest.

*Fledging.*—At Pajaro, we found unfledged chicks between 27 April and 9 September. We determined the fledging period for 22 chicks (from hatching to a first flight of at least 3 m) at no more than 29 to 33 days ($\bar{x}$ = 30.9); at least 15 appeared unable to fly at 29 days. Subsequent to this study 3 chicks fledged at 28 days. Two captive chicks studied by Boyd (1972) took 28 and 32 days to fledge. Thus, it appears the Snowy Plover requires four to four and one-half weeks to fledge. Rittinghaus (1956, 1975) gives an average of 41 days for Kentish Plovers on Oldeoog and 27 and 32 days for two young at Amsterdam. Cramp and Simmons (1983), aware of these differences, feel 27 to 31 days is the more likely fledging period.

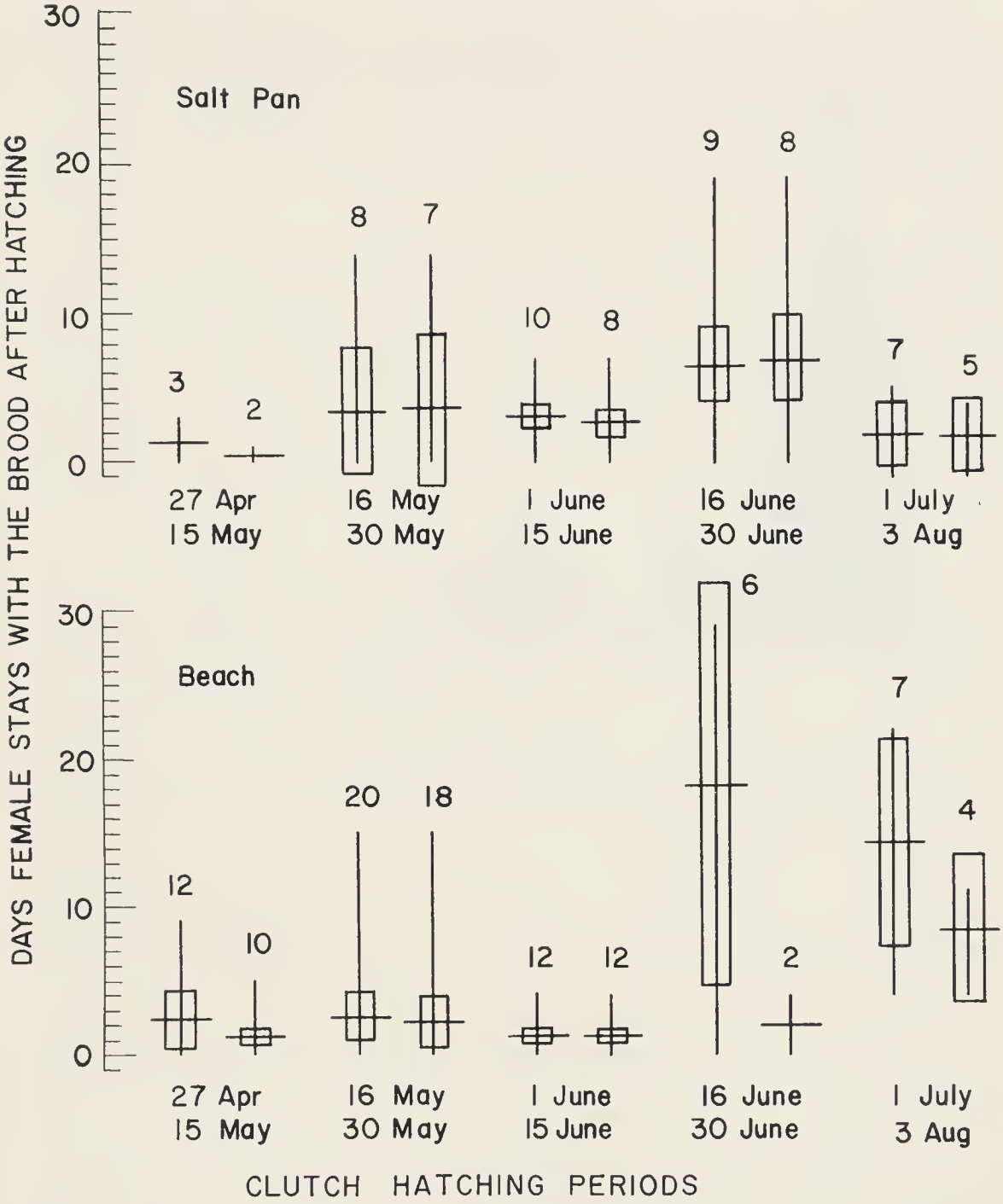


FIG. 5. Number of days the female remains with the brood after the chicks hatch at the Pajaro beach and salt pan. Data are broken into five clutch-hatching periods. For each period the left component of a data set includes all 6 years and the right component includes all years except 1977. The vertical line is the range, the horizontal line the mean, and the rectangle the 95% confidence interval of the mean; sample sizes are above.

Although both sexes attended Snowy Plover broods, the female usually deserted before the young could fly (Fig. 5). Females had deserted by the sixth day in 17 of 21 early salt-pan broods, 13 of 16 late salt-pan broods, and 40 of 44 early beach broods, using a 15 June hatching date to divide the periods. In contrast, only three had left by the sixth day in 13 late-

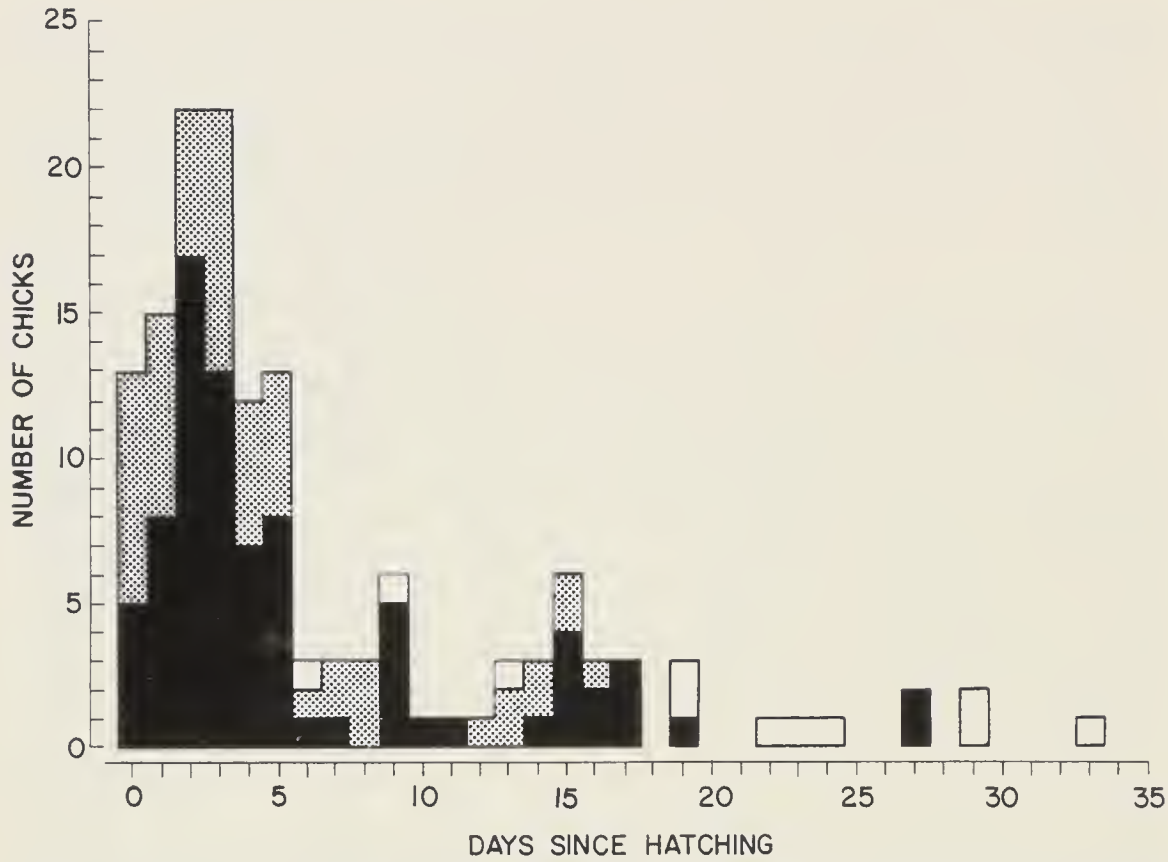


FIG. 6. Age of chicks lost during fledging at Pajaro. Solid areas represent the beach and stippled areas the salt pan. Blank areas represent periods (from either location) of chicks last seen when fledging was not certain.

season beach broods. Seven of 10 females that remained for more than six days with the late beach broods did so in 1977; all stayed for more than 20 days, longer than any other female with a brood that had not been deserted by the male. In 1977, a year with high reproductive success, the north spit nesting area was small, and nests hatched in rapid succession with as many as eight broods sharing a 6.8-ha area. Parents from neighboring broods clashed with each other frequently, leading us to suspect that both parents may have been needed to keep track of their chicks or to prevent them from being attacked by neighboring adults. Such long-term sharing of fledging duties was unusual, as at Pajaro in other years. And at other locations we found that only the male usually cared for the young after they were a few days old. Males usually accompanied chicks until they were 29 to 47 days old. In three additional cases, females that were deserted by mates from seven days before to six days after the eggs hatched, cared for the broods alone: two fledged young from these broods.

Broods rarely remained in the nesting territory until fledging, although they sometimes remained in the general area. Broods crossed other birds' territories, sometimes causing neighbors to attack the young, and at least

once causing abandonment and death of a chick. Despite this, there were two cases of chick adoption, with chicks incorporated into the broods of foster parents by the time the adopted chicks were nine days old. Adoption of young by the Killdeer (Lenington 1980) and by the Wilson's Plover (*Charadrius wilsonia*) (Bergstrom 1982) are also reported to occur on rare occasions.

Most chick mortality occurred before chicks were six days old (Fig. 6). In at least 15 of 29 cases in which all three young in a brood were lost, all chicks disappeared on the same day. At least 92.7% of the 124 chicks reaching 16 days of age fledged. Predators and encounters with other birds were the only causes of chick mortality we witnessed. Loggerhead Shrikes (*Lanius ludovicianus*) took at least 14 chicks at the salt pan in 1979. Another chick at the salt pan failed to leave with the rest of the brood after its parents had a 14-min confrontation with a pair of American Avocets (*Recurvirostra americana*) and their brood.

*Second broods and polygamy.*—Some Snowy Plovers attempted second broods at Pajaro. Females initiated second nesting attempts with different males after deserting their first broods and mates. Males, and rarely females, attempted second broods after successfully fledging young from a previous brood. Sixty Pajaro females abandoned broods before 1 July and had time for further breeding. Seventeen renested with new mates at Pajaro, four at the evaporation ponds, and one at Wilder State Beach. Five formed pair bonds with new mates and disappeared, and 32 left unmated, but stayed away at least 38 days (long enough for a successful nesting attempt). The remaining female, which had laid three clutches previously, was absent only 13 days and may not have attempted a new nest.

Twelve of 16 marked males at Pajaro that had fledged chicks early enough for a subsequent successful nesting attempt either renested or were thought to have done so; the status of the other 4 males was unknown. Five of the 12 renested at Pajaro (only one in its original territory) and three at the evaporation ponds; the other four were found paired at the evaporation ponds, but their nests were never found. Ten of the 12 had acquired new mates by the time their chicks were 29 to 38 days old, and two paired on unknown dates. In seven instances the male deserted his brood first, but in at least four others, he continued to tend his chicks during the early part of courtship. All second mates were acquired by 2 July.

Two additional males paired and renested with new females before their chicks from the first nest had fledged. One male's second nest had its first egg when his first brood was only 29 days old. Another male was helping with the incubation of a new three-egg clutch by the time his two

chicks, which he still brooded, were 25 days old. The male struggled to brood and incubate nightly, with the chicks elevating him well above the eggs. They fledged when 32 days old, and at 34 days flew away, but returned each evening and were brooded on the nest until they were 38 days of age. The only female that both tended a brood alone and acquired a new mate did so when her two chicks were 26 days old.

On 27 occasions, banded males losing broods still had time for a second attempt at nesting. We are certain that renesting occurred at Pajaro or the evaporation ponds on 13 occasions, and it probably took place five additional times at the evaporation ponds as well. In eight instances, males left the area with time left for an attempt elsewhere. One male that lost a brood in late June definitely failed to renest.

The above examples describe a serially polygamous breeding system that differs little from a monogamous double-brooded one, except that the second broods of both sexes were with new mates. Polygyny occurred rarely, although the previously discussed clutches of five and six eggs at Big Lagoon may have represented polygyny as did the following: a banded male, nesting with a banded female, was observed courting a different female in a different part of the salt pan. Nine days later, we found him on a one-egg clutch, 110 m from his other nest, and seven days later we captured him on the new nest. When his first clutch hatched, he and his first mate attended the chicks. His second nest was destroyed by a predator two days later. In addition, we saw or captured males on others' nests at least three times. Because male Snowy and Kentish Plovers (Rittinghaus 1956) sometimes sit on another's eggs, caution is necessary when documenting polygyny.

*Breeding success.*—Yearly variation in Snowy Plover breeding success at Pajaro is summarized in Table 1. Combining areas over the six years, we calculated a clutch-hatching rate of 58.2% (N = 189), an egg-hatching rate of 55.2% (N = 534), a chick-fledging rate (percent of hatched chicks fledged) of 39% to 42% (N = 296), and a production rate of 0.8 to 0.9 fledged young per female (N = 151). Over all years, 94.5% of the 293 eggs from successful nests hatched. Six eggs were deserted with a large living embryo, one with a large dead embryo, eight were rotten without evidence of an embryo, and one was not checked.

*Return rate, survival rate, and sex ratio.*—Mortality and degree of site fidelity are the two factors that affect return rates of migratory birds to specific breeding areas in consecutive years. We determined that at least 78.6% of 56 male and 72.6% of 73 female breeding Snowy Plovers were alive at least one year after being banded on the nest (or after laying the first egg for those banded prior to nesting). Of the surviving males, 34 nested in the banding location in the second year, eight were seen but

TABLE 1
REPRODUCTIVE SUCCESS OF SNOWY PLOVERS DURING SIX YEARS

| Year | Est. no.[a] of | | Total no. of clutches[a] | % successful clutches/ % eggs hatched | Eggs hatched per | | Percent young fledged[b] | Young fledged per | |
|---|---|---|---|---|---|---|---|---|---|
| | females | males | | | female | male | | female | male[b] |
| 1977 | 25 | 23 | 27 | 85/74 | 2.4 | 2.6 | 75–83 | 1.8–2.0 | 2.0–2.2 |
| 1978 | 24 | 24 | 36 | 50/47 | 1.9 | 1.9 | 20–27 | 0.4–0.5 | 0.4–0.5 |
| 1979 | 26 | 22 | 43 | 53/53 | 2.5 | 3.0 | 26–29 | 0.7 | 0.8–0.9 |
| 1980 | 13 | 14 | 21 | 38/40 | 1.7 | 1.6 | 18–19 | 0.3 | 0.3 |
| 1981 | 23 | 24 | 31 | 58/51 | 2.0 | 1.9 | 63–67 | 1.3 | 1.2–1.3 |
| 1982 | 23 | 24 | 31 | 65/63 | 2.4 | 2.3 | 20 | 0.5 | 0.5 |

[a] Includes 6 clutches inferred from broods and excludes 4 clutches we accidentally destroyed.
[b] Minimum and maximum possible because of the uncertain fate of some chicks.

were not known to nest in the banding area the second season, one returned after the breeding season, and one, not known to return to Pajaro, was located at another area. Comparable figures for females were 30, 15, 3, and 5. Thus 65.8% of 73 females and 76.8% of 56 males were in the breeding area one or more years after banding, and 6.8% of the females and 1.8% of the males were outside the breeding area.

Females may be less site-faithful and have lower survival rates than males, but this cannot be demonstrated with our small samples. We can estimate the sex ratio of the population if we assume that (1) our survival estimates are accurate, (2) the population size is stable, and (3) the proportion of males and females hatching and reaching breeding age is the same, from the following equation:

$$\frac{1 + S_m + S_m^2 + S_m^3 + \ldots + S_m^n}{1 + S_f + S_f^2 + S_f^3 + \ldots + S_f^n}$$

Where $S_m$ (0.786) is the annual adult male and $S_f$ (0.726) is the annual adult female survivorship applied each year (1, 2, . . . , n), and $S_m^n$ and $S_f^n$ approach zero. The predicted ratio is 1.28 males per female.

At Pajaro, males typically outnumbered females during the breeding season. For example, on 15 May 1980, 1981, and 1982, the number of males to females was 8:7, 24:22, and 19:16, respectively. On 15 June 1980, 1981, and 1982, it was 8:5, 14:7, and 12:6, respectively; however, a larger population is needed to measure sex ratio. This was available at Mono Lake, where one of the state's largest breeding populations occurs (Page and Stenzel 1981).

Our results from two seasons of adjusted censuses at Mono Lake were similar. In each year males outnumbered females on all 10 censuses, a

result which differed significantly from equality (Wilcoxon matched-pairs signed-ranks test, $P = 0.0010$). Adjustment factors calculated from the color-marked bird sightings revealed fewer males were overlooked at Mono Lake because their behavior made them easier to see. For 1981, we calculated an average of 1.901 marked males and 2.951 marked females were present for each one found on a census. As some marked birds were seen more than once on a census, we assumed overcounts of unmarked birds were also probable. We calculated that only 0.844 of the males and 0.949 of the females on censuses were different birds. Combining factors, we concluded there were (1.901 × 0.844 =) 1.604 males, and (2.951 × 0.949 =) 2.800 females for each one counted (whether duplicate or not) in 1981. Our results in 1982 were similar, with (1.859 × 0.905 =) 1.682 males and (3.333 × 0.966 =) 3.220 females for each one counted. This difference in detection rates was undoubtedly due to the difficulty of finding the females, which incubated most of the day on widely scattered nests from which they attempted to depart undetected when approached. By contrast, males concentrated around feeding areas where they were easily observed. The average number (from adjusted totals) of males was 115.3 (SE = 5.3) and females 82.3 (SE = 2.7) in 1981, and in 1982, 119.1 (SE = 7.0) males to 85.3 (SE = 7.4) females for a M:F ratio of 1.40:1 in each year.

## DISCUSSION

The polygamous, double-brooded breeding system described for Snowy Plovers at Pajaro is probably commonplace in *C. alexandrinus* west of the Rocky Mountains. Our findings at Pajaro were corroborated by observations of banded breeding birds at Wilder Beach, Mono Lake, and, subsequent to this study, at two other sites on Monterey Bay (unpubl. data).

*Comparison with other C. alexandrinus.*—Snowy Plovers at Cheyenne Bottoms, Kansas, differ from those west of the Rockies mainly by being monogamous single-brooders, with both sexes caring for the young (Boyd 1972, in litt.). All individuals in this population are migrants; the earliest arrivals reaching the breeding grounds in the beginning of April. Most clutches are laid between late May and late June. An exceptionally early clutch was started on 22 April and the last on 26 June, giving a maximum interval for clutch initiation of 65 days. As about 58 days elapse between laying the first egg and fledging of the young at Cheyenne Bottoms, the length of the breeding season is scarcely long enough for males to participate in double broods. Because egg laying is concentrated in June at Cheyenne Bottoms, there is not time for most females to initiate second clutches, even if they were to desert the first one at hatching. Boyd (1972) believes that high water levels do not allow for earlier nesting.

We noted a few other differences between Snowy Plovers at Cheyenne Bottoms and Pajaro. Although Boyd (1972) states that the female incubates during most of the day, we differ on the sex of the nocturnal incubators. On three occasions he determined that only the female incubated at night, drawing his conclusion from an electronic device that indicated when birds got on and off the nest. This differs from patterns at Pajaro and Mono Lake, and from the Kentish Plover, which Rittinghaus (1956) and Nakazawa (1979) characterize as being mainly female by day and male by night.

The behavior of the off-duty parent also differed between Cheyenne Bottoms and our study locations. At Cheyenne Bottoms, Boyd (1972) reports that "throughout the period that the female was on the nest the male could be seen standing 20 m to 30 m away." Males preened, slept, or at other times fed near the water's edge. At Pajaro and Mono Lake, males were not within sight of their nests during much of the day. The difference might be related to the distance between nesting and feeding areas at the two locations.

Snowy Plovers at Pajaro differed from Kentish Plovers at Oldeoog in several major ways. Unlike Snowy Plovers, Kentish Plovers at Oldeoog typically attempt a single brood, although in rare instances two broods are known (Rittinghaus 1956). Rittinghaus reports that, for two years in a row, one female successfully incubated a clutch with one male and, after the young hatched, paired with another male and successfully reared a brood with him. This was a common pattern at Pajaro. Rittinghaus (1956, 1961, 1975) is not clear as to the duration of the egg-laying period at Oldeoog, so we do not know if the period extends long enough for double brooding to be probable. Some female Kentish Plovers desert first broods and renest with new mates at the Camargue in southern France, where the egg-laying period of the plover population spans three months (Lessells 1984).

Rittinghaus's 1956 and 1975 reports differ on parental roles in the rearing of broods. In the 1956 paper he states that the parents initially share responsibility equally, though at times only one parent takes on most of the chick-tending duties. The female's share generally increases toward the end of the fledging period, and in late broods the female usually tends the young while the male joins large flocks of successful pairs with their fledged young. This differs from the Snowy Plover, and from Rittinghaus's 1975 Kentish Plover report in which he states that the young, though cared for by both parents during the first two weeks, are cared for normally by the male when only one parent is with the brood. Cramp and Simmons (1983) add to the confusion by reporting that one parent leaves the chicks when they are half-grown, but that the sex of the departing parent varies with location: in Amsterdam more males than fe-

males stay with the young, but at Oldeoog more females than males stay with the young. At the Camargue, female Kentish Plovers normally desert the brood a week after hatching, although there are instances of male desertion (Lessells 1984). At Pajaro, female Snowy Plovers typically had left the brood by the time the young were 6 days old.

The prolonged period of biparental brood care at Oldeoog may be a consequence of the extremely high density of nesting birds—96 pairs on 0.7 ha in 1948 (Rittinghaus 1975). The only time females remained with broods for extended periods at Pajaro was on the beach in 1977 when we had our highest density of active nests and broods. High breeding density, which might reduce food availability and increase the rate of antagonistic interactions between broods, may cause the lengthy 41-day Kentish Plover fledging periods (Rittinghaus 1956, 1975), which are at least 10 days longer than for Snowy Plovers at Pajaro or Cheyenne Bottoms (Boyd 1972).

*Factors underlying polygamy in Snowy Plovers.*—New mates are apparently available to female Snowy Plovers because of a breeding population with surplus males. The skewed sex ratio could arise in several ways; we have no data that would eliminate any of the various possibilities. As demonstrated earlier (see Results), small differences in survival rates of breeding male and female Snowy Plovers by themselves could be sufficient to account for the asymmetry. The differences in survival rates could, in turn, be accounted for by differences in the sexes' exposure to risks or in effort expended due to the different parental roles.

Sequential polyandry could also occur in the absence of an absolute difference in the sex ratio if (1) females indirectly limit access of other females to males via territoriality; or (2) directly limit access by guarding more than one mate (Oring 1982); or (3) if males breed at an earlier age than females. We found no evidence that females or guarded males defended territories occupied by more than one male. Furthermore, females bred at as early an age as males. We found nests or broods for 10 of 15 first-year males (banded as chicks) and 9 of 14 first-year females on Monterey Bay. The first egg in nests of three males was laid when they were 308, 326, and 358 days old (measured from hatching date) and those of three females when they were 267, 308, and 354 days old.

With a surplus of males when females were physiologically ready for second broods, it could be advantageous for females to leave brood care solely to their mates, and then start another nesting attempt with a new partner. In contrast, a male would have little to gain from abandoning broods to a female's care; his chances for new mates would be limited by the unfavorable sex ratio. The advantage of brood desertion by females would be particularly clear when uniparental care was not a serious constraint in raising young, and when the chance for fledging two broods in

one season was increased by minimizing the number of days spent with the first brood. Uniparental brood care is widespread in plovers (Bunni 1959, Hussell and Page 1976, Bergstrom 1982, this study) and other shorebirds (Jenni and Collier 1972, Oring and Knudson 1972, Pitelka et al. 1974). We believe the females' emancipation from brood-rearing duties increased their chances for double broods. Although the breeding season was long enough for double brooding with the same mate, the high rate of clutch destruction often necessitated one or more replacement clutches before a female hatched a brood. As the extra time needed for the replacement clutch greatly reduced the time available for second broods, any mechanism that allowed females to start second clutches sooner would increase the chances of two broods fledging.

This raises the question of why Snowy Plover females do not desert initial clutches sooner than they do. Female Spotted Sandpipers (*Actitis macularia*) desert clutches during the incubation period (Oring and Knudson 1972), and females of other polyandrous species such as the Red Phalarope (*Phalaropus fulicaria,* Schamel and Tracy 1977), Red-necked Phalarope (*P. lobatus,* Hildén and Vuolanto 1972), and Northern Jacana (*Jacana spinosa,* Jenni and Collier 1972), or of multi-clutch species such as the Mountain Plover (*Charadrius montanus,* Graul 1975) and Temminck's Stint (*Calidris temminckii,* Hildén 1975) desert clutches as soon as they are completed. The ability to implement a single-parent incubation scheme is an important factor promoting their breeding systems. In contrast, Snowy Plover adults remaining after mates had deserted or died typically deserted the clutch unless it was 10 or fewer days to hatching.

Other species that make more than one breeding attempt per season do so monogamously. For example, monogamously established pairs of Killdeers and Wilson's Plovers produce multiple clutches sequentially, and females are frequently emancipated from brood-rearing duties for second clutches (Bunni 1959, Bergstrom 1982), demonstrating that these males can rear broods alone. It would be valuable to know whether the sex ratios differ from equality in these species. The females may remain with the first broods only because surplus males with which they could start second broods are not available. This hypothesis implies that in the Snowy Plover serial polyandry may simply be a facultative response to the conditions of a skewed sex ratio. The key evolutionary step to this mode of reproduction would then be the female's ability and tendency to make more than one breeding attempt per season.

The only other shorebird known to employ this type of polyandrous strategy is the Dunlin (*Calidris alpina schinzii*) in Finland (Soikkeli 1967). Typically, Finnish female Dunlins desert first broods about six days after hatching and after a few more days leave the breeding area. In one of six

years, however, when nesting commenced very early, three females undertook second broods with new mates. None of these males had yet bred that season (Soikkeli 1967). The Dunlin's polyandry also appears to be a facultative response to an elongated breeding season and to the availability of additional mates.

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# TEMPORAL DYNAMICS OF NEOTROPICAL BIRDS WITH SPECIAL REFERENCE TO FRUGIVORES IN SECOND-GROWTH WOODS

THOMAS E. MARTIN AND JAMES R. KARR[1]

ABSTRACT.—Birds were mist-netted and banded in a second-growth woodland in central Panama to examine temporal dynamics of capture rates and to examine if these dynamics reflected presence or absence of transient birds. Capture rates of frugivores fluctuated much more than insectivores; nectarivores were intermediate in their fluctuations. Consequently, insectivores were recaptured more frequently than frugivores, indicating greater spatial stability. Species within a guild differed in their recapture frequencies, but unstable species with low recapture frequencies were most often frugivores; stable species with high recapture frequencies generally were insectivores. Migrants exhibited the same patterns as nonmigrants of the same guild. Examination of two common nonmigrant frugivore species showed that fluctuations in capture rates were due mostly to movements by transient immatures or females. Capture rates of nonmigrant frugivores declined markedly during late March. The decline may be due to movements in response to an influx of migrants during spring migration, habitat switching, or microclimatic conditions. This study provides evidence that some tropical birds are highly dynamic and that such dynamics reflect transience in addition to other population processes. *Received 26 Apr. 1985, accepted 28 Aug. 1985.*

Evidence is accumulating that local abundances of a wide variety of tropical organisms, including plants (Hartshorn 1978, Brokaw 1982, Garwood 1983), insects (Janzen 1973; Willis 1976; Wolda 1977, 1978, 1980; Tanaka and Tanaka 1982), frogs (Toft 1980), and lizards (Sexton 1967, Sexton et al. 1971, Ruibal and Philibosian 1974, Schoener and Schoener 1980) vary markedly over time. Abundances of tropical forest birds also are temporally variable (Karr 1976a, 1981a, Karr et al. 1982, Faaborg 1982, Karr and Freemark 1983, Faaborg et al. 1984). Moreover, temporal variance may be greater for birds in young second-growth woods than in older forest and greater for tropical birds that rely on variable food types (Karr 1976a). With the exception of Karr (1976a), studies of tropical bird dynamics have focused on birds in older forests. Yet, young forest is an increasingly common habitat in the neotropics (Myers 1979, 1981). As many species of migrant birds from North America often concentrate in young forest, especially during migration (Willis 1966, Karr 1976b, Chipley 1977, Hutto 1980, Johnson 1980, Martin 1985a), young forest provides an opportunity to compare population fluctuations of both migrants and nonmigrants.

[1] Dept. Ecology, Ethology, and Evolution, Univ. Illinois, Champaign, Illinois 61820. (Present address TEM: Dept. Zoology, Arizona State Univ., Tempe, Arizona 85287; Present address JRK: Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama.)

Temporal variance in abundances can be caused by population recruitment and mortality. Short-term (e.g., <3 months) fluctuations in abundances, however, can be caused by movement of individuals into or out of a locality. Movements by individuals are thought to be an important cause of the variance in tropical bird abundances (e.g., Karr and Freemark 1983), but no one has tested directly whether fluctuations in bird abundances actually reflect occurrence of transients in a locality. A direct test can be made by banding birds and examining frequencies of recaptures; residents have a higher probability of recapture than transients. Consequently, if short-term fluctuations in abundances are caused by movement of transients, then recapture frequencies should be lower for those groups of birds that exhibit greater variation in abundances. Second, increases in abundances should be associated with greater numbers of transients and especially during seasonal periods when recruitment can not be a cause of population increase. Third, if fluctuations in abundances reflect movements due to variability of food resources, then birds that rely on more variable food types should show greater fluctuations in abundances and lower recapture frequencies. Furthermore, this prediction should hold for both migrants and nonmigrants with the same food habits.

We examined these predictions based on a study of birds in a young second-growth forest in Panama during which we captured over 1500 birds in nearly 6000 mist-net h. Variations in capture rates are compared among groups of birds of similar food habits (i.e., frugivores, insectivores, nectarivores) to examine dynamics as a function of resources. We emphasized frugivores because they represented the dominant portions of both migrant and nonmigrant populations. We compared recapture frequencies of banded birds to provide a direct test of whether variable capture rates reflect movements of birds. In addition, we examined recapture frequencies and capture rates of the transient and resident portions of the populations of the two most common nonmigrant species to determine if variation in capture rates reflected occurrence of transients.

## METHODS

*Bird sampling.*—We used mist nets (12-m long, 4 shelves, 30-mm mesh) to sample birds within a 4.5-ha second-growth woodland in Parque National Soberania, Panama. Abundances of birds were indexed based on capture rates (numbers of birds captured per 100 mist-net h). Relative abundances of birds represented in samples of standard number of captures were not used; relative abundances are dependent on representation of other birds in the sample and transients may be overrepresented (Van Remsen and Parker 1983). Capture rates are independent of the representation of other birds in the sample and, thus, more accurately reflect changes in actual abundances.

Birds were netted during the early (January) and late (March) dry seasons of 1980 and 1981. We used two lines of mist nets in 1980. One line included 6 nets and was operated

from 7 to 14 and from 20 to 23 January and from 16 to 27 March. A second line, approximately 30 m away, included 7 nets and was operated from 16 to 23 January and from 19 to 27 March. Both lines were operated from 9 to 22 January and 18 to 28 March 1981. Two additional lines, with 9 and 8 nets each, were operated from 23 January to 3 February and from 6 to 12 March 1981. Nets usually were operated from 06:15 to 17:30 h, when weather permitted, and checked every hour. Capture rates were calculated from the first 6 days of each netting period to standardize length of time each net was operated. Nets generally were operated longer than 6 days, however, to increase the number of captured and banded birds.

Paired net lines were operated in each sampling period as a check on adequacy of sample size. Temporal patterns should be the same for both lines of a pair if netting provides a reliable sample. As chi-square analyses showed no significant differences in species numbers or abundances between lines within a pair, data from paired lines were pooled. Two lines were added in 1981 to obtain additional data for different portions of the dry season (a later stage of early dry season and an earlier stage of the late dry season-premigration). New net lines were established because capture rates decline over time (Terborgh and Weske 1969, Karr 1979) and use of the same sites in late and early January could bias results.

All captured birds were banded with a numbered aluminum band except hummingbirds. For hummingbirds, we clipped the first primary to allow determination of recaptures within a sample period. Recaptures between sample periods could not be determined due to intervening molts.

Each net line was operated until at least 100 different individuals were captured during each sampling period. Birds recaptured during a single sampling period were not considered to be different individuals. Recaptures from previous periods were included in the 100-bird totals. Overall, 1518 birds were captured in 5994 net h.

We classified bird species into food habits groups based on Karr (1971), Wetmore (1965, 1968, 1972), and personal observations. Species that changed food habits, such as migrants, were classified based on the food category that constituted the major portion of their diet during the period they were present on the area. Comparisons of abundances or species richness among samples are based on Chi-square or Fisher's Exact Probability tests. Comparisons were made using the number of individuals or species captured and corrected by the sample effort (mist-net h).

*Vegetation.*—Vegetation was sampled using the point sampling method of Karr (1971). Points were sampled along two transects that ran parallel to each mist net; one transect was on each side and about 2 m from each net. Each transect included 20 points. Vegetation on lines 1 and 2 was similar (Fig. 1) with the canopy peaking mostly at 5 m, but with a few emergent *Didymopanax morototoni.* Vegetation was taller along lines 3 and 4 with the canopy peaking mostly at 7.5–10 m. Nevertheless, the vegetation was remarkably similar on each plot; below 5 m, foliage densities were similar for all lines.

*Weather.*—January through March are the driest months of the year in central Panama (Croat 1978). Total rainfall for these three months is generally around 11.4 cm (Table 1). The dry season (January–March) of 1980 was slightly wetter than average and the dry season of 1981 was much wetter than average, due especially to record rainfall in January; March also was slightly wetter than normal (Table 1).

## RESULTS

*Numbers of species.*—We captured a total of 76 species in 1980 (52 species in January; 60 species in March) and 84 species in 1981 (57 in January; 69 in March). The two annual samples totaled 101 species. We

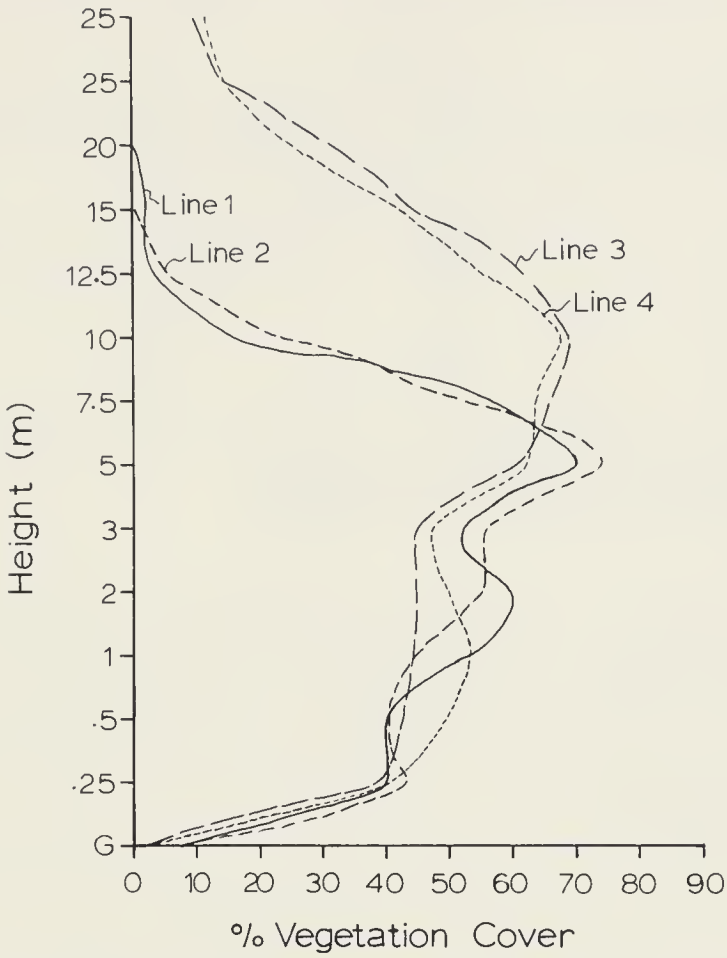


FIG. 1. Foliage profiles for the four net lines based on percent vegetation cover at increasing heights.

observed 136 species on the study area, overall, and considered 96 to be regular dry-season residents based on capture or observation of individuals in at least 3 periods of the study (Appendix 1). Additional species were not captured because their activities were restricted to the canopy. A higher ($P < 0.01$) percentage of species and individuals were migrants in late March than in January of both years (Fig. 2) due to spring migration.

*Early January vs late March.*—Capture rates of nonmigrant, migrant, and total insectivores did not change ($P > 0.10$) from January to late March in either year (Fig. 3). Nectarivores increased in March in 1980 ($P < 0.10$) and 1981 ($P < 0.01$). Nonmigrant frugivores decreased ($P < 0.001$) while migrants increased ($P < 0.001$), resulting in no difference ($P > 0.10$) in capture rate of all frugivores between months.

*Late January vs early March.*—Capture rates of migrant and nonmigrant insectivores did not change ($P > 0.10$) from late January to early March (Fig. 3). Nectarivores showed an increasing trend, but the increase was not significant ($P > 0.10$). Nonmigrant frugivores increased ($P <$

TABLE 1

MEAN RAINFALL (CM) FOR THE THREE DRY SEASON MONTHS FOR 1924–1962 (FROM CROAT 1978), 1964–1980 (FROM PANAMA CANAL COMMISSION CLIMATOLOGICAL CENTER), AND FOR THE TWO YEARS OF THIS STUDY

| | January | February | March |
|---|---|---|---|
| 1924–1962 | 5.6 | 3.3 | 3.1 |
| 1964–1980 | 6.4 | 2.5 | 2.5 |
| 1980 | 11.9[a] | 4.8[c] | 0.5[b] |
| 1981 | 39.9[c] | 2.0 | 6.1[c] |

[a] Rainfall significantly different ($P < 0.05$) from the 1964–1980 mean.
[b] Rainfall significantly different ($P < 0.01$) from the 1964–1980 mean.
[c] Rainfall significantly different ($P < 0.001$) from the 1964–1980 mean.

0.05) from late January to early March. In fact, capture rates of nonmigrant frugivores were greater in early March than in early January ($P < 0.001$), late January ($P < 0.05$) or late March ($P < 0.001$) due to an increase from January through early March and a subsequent decline in the latter half of March (Fig. 3).

*Between-years.*—Capture rates of nonmigrant insectivores were less ($P < 0.05$) in 1981 than in 1980 in both months (Fig. 3). Nectarivores did not differ between years ($P > 0.10$) in either month, while capture rates of frugivores were markedly less ($P < 0.001$) in both months of 1981 than in 1980 for migrants and nonmigrants. In summary, frugivores exhibited greater within-season and between-year shifts in capture rates than other guilds.

*Influence of common species.*—Changes in importance of guilds were due, in part, to shifts in capture rates of the most common community members (Appendix 1). The frugivorous Red-capped Manakin, Golden-collared Manakin, and Ochre-bellied Flycatcher (scientific names are provided in Appendix 1) had the highest capture rates in January of both years and early March 1981. Capture rates of all three frugivores declined significantly in late March of both years (Table 2). They were replaced by Long-tailed Hermit, Swainson's Thrush, and Tennessee Warbler as the most abundant species (Table 2).

The increase in Swainson's Thrush and Tennessee Warbler reflected the increase in migrant frugivores in late March (Fig. 3). Capture rates of the three nonmigrant frugivore species did not reflect capture rates of all (migrant and nonmigrant) frugivores (Fig. 4) because these three species decreased in late March when the influx of migrants kept total frugivore capture rates constant (see above). Capture rates of each of these three frugivore species showed the same temporal trend as all nonmigrant fru-

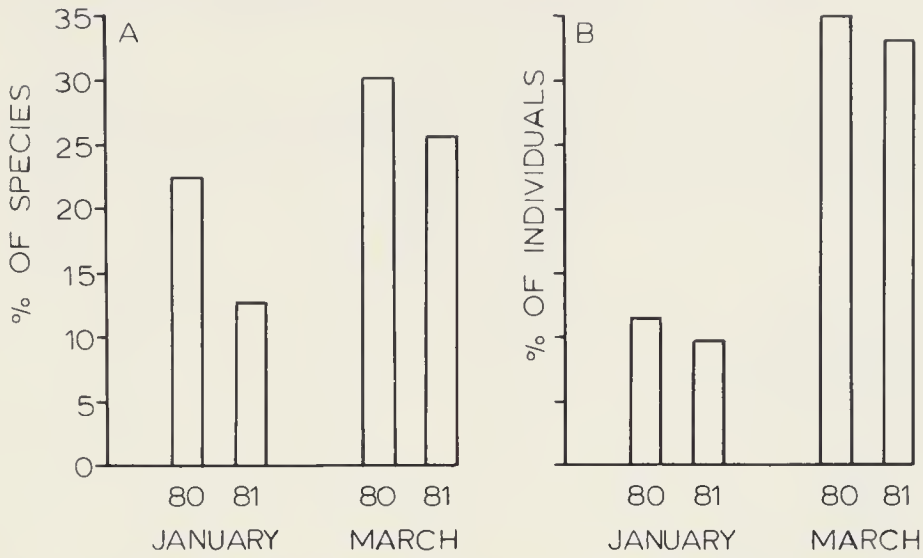


FIG. 2. Percent of species (A) and individuals (B) that were migrants in 200-bird samples in January and March of 1980 and 1981.

givores, increasing from January through early March, and decreasing in late March (Table 3) (Fig. 4). Furthermore, the decrease in nonmigrant frugivores in late March was not due simply to the three dominant species; abundances of all other nonmigrant frugivores also declined from January to late March (Table 2).

The increase in Long-tailed Hermits apparently was the primary cause

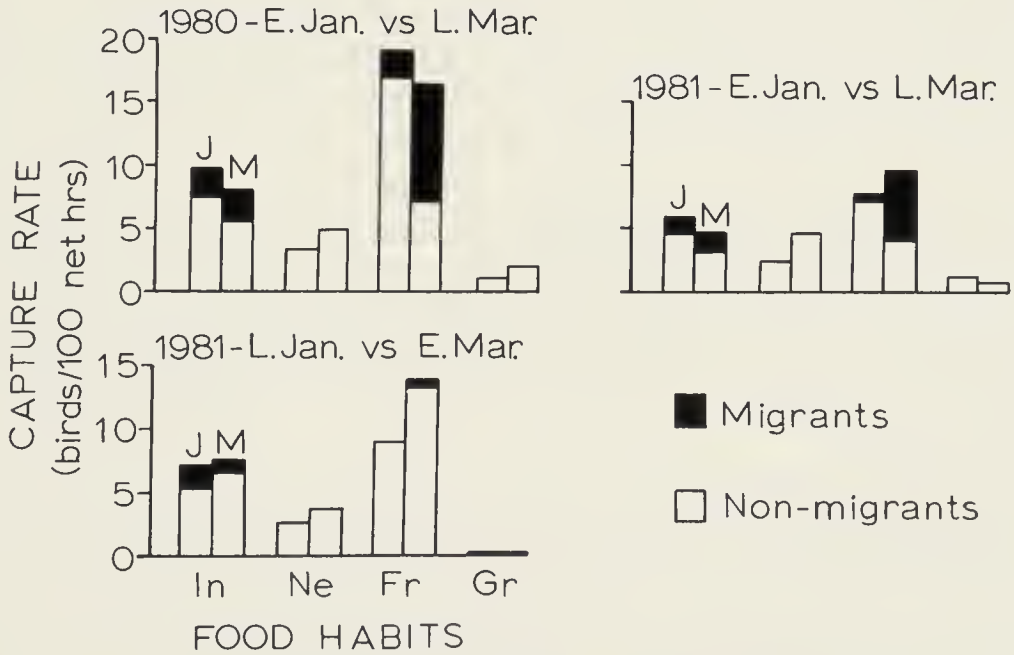


FIG. 3. Changes in capture rates of guilds in 200-bird samples from early January to late March (mist-net lines 1 and 2) in 1980 and 1981 and from late January and early March (mist-net lines 3 and 4) in 1981. Guilds include insectivores (In), nectarivores (Ne), frugivores (Fr), and granivores (Gr).

TABLE 2

CHANGES IN NUMBERS OF INDIVIDUALS CAPTURED FOR THE MOST COMMON SPECIES AND FOR NONMIGRANT FRUGIVORES AND NECTARIVORES WHEN THESE COMMON SPECIES ARE SUBTRACTED FROM 200-BIRD SAMPLES FROM JANUARY TO LATE MARCH OF 1980 AND 1981

| | 1980 | | 1981 | |
|---|---|---|---|---|
| | January | March | January | March |
| Red-capped Manakin | 25 | 15[a] | 27 | 7[c] |
| Golden-collared Manakin | 38 | 17[c] | 23 | 14[a] |
| Ochre-bellied Flycatcher | 22 | 6[c] | 10 | 6 |
| Long-tailed Hermit | 2 | 9[a] | 10 | 24[b] |
| Swainson's Thrush | 1 | 8[b] | 3 | 18[c] |
| Tennessee Warbler | — | 23[c] | — | 24[c] |
| Other nonmigrant frugivores | 18 | 9[a] | 29 | 19[a] |
| Other nectarivores | 18 | 22 | 20 | 20 |

[a] Significantly different ($P < 0.05$) using a binomial probability test and correcting for differences in numbers of net h.
[b] Significantly different ($P < 0.01$) using a binomial probability test and correcting for differences in numbers of net h.
[c] Significantly different ($P < 0.001$) using a binomial probability test and correcting for differences in numbers of net h.

of the increase in nectarivores; abundances of the other nectarivores changed little between months (Table 2). Finally, insectivore abundances were not influenced by any dominant species; no insectivore species contributed more than 6 individuals to any 200-bird sample (Appendix 1).

*Spatial constancy.*—If shifts in capture rates reflect transience, then insectivores should have higher recapture frequencies than frugivores because of the greater temporal variance of frugivores (see above). Recaptures between months and years were higher for insectivores than for frugivores (Fig. 5). Moreover, these trends hold when individual species are examined; more ($P < 0.013$) insectivore species (13 of 16) had recapture frequencies of 40% or greater between months than frugivore species (2 of 12) (Table 4). Also, more ($P = 0.039$) insectivore species (11 of 14) had recapture frequencies of 40% or greater between years than frugivore species (3 of 12). The low recapture frequency of frugivores suggests transience. Presence of transients was examined for the two manakin species.

*Golden-collared Manakin.*—A total of 164 Golden-collared Manakins was captured during this study (Table 5). Recapture rates between months and years were much higher for adult males than for immatures or females (IOFs) (Table 5). Also, a higher percentage of captures within a month were recaptures from previous months for males than for IOFs. All adult males that were banded in 1980 and recaptured in 1981 were recaptured on the same lines where originally banded. New lines were established in late January 1981, and any recaptures during this period are individuals

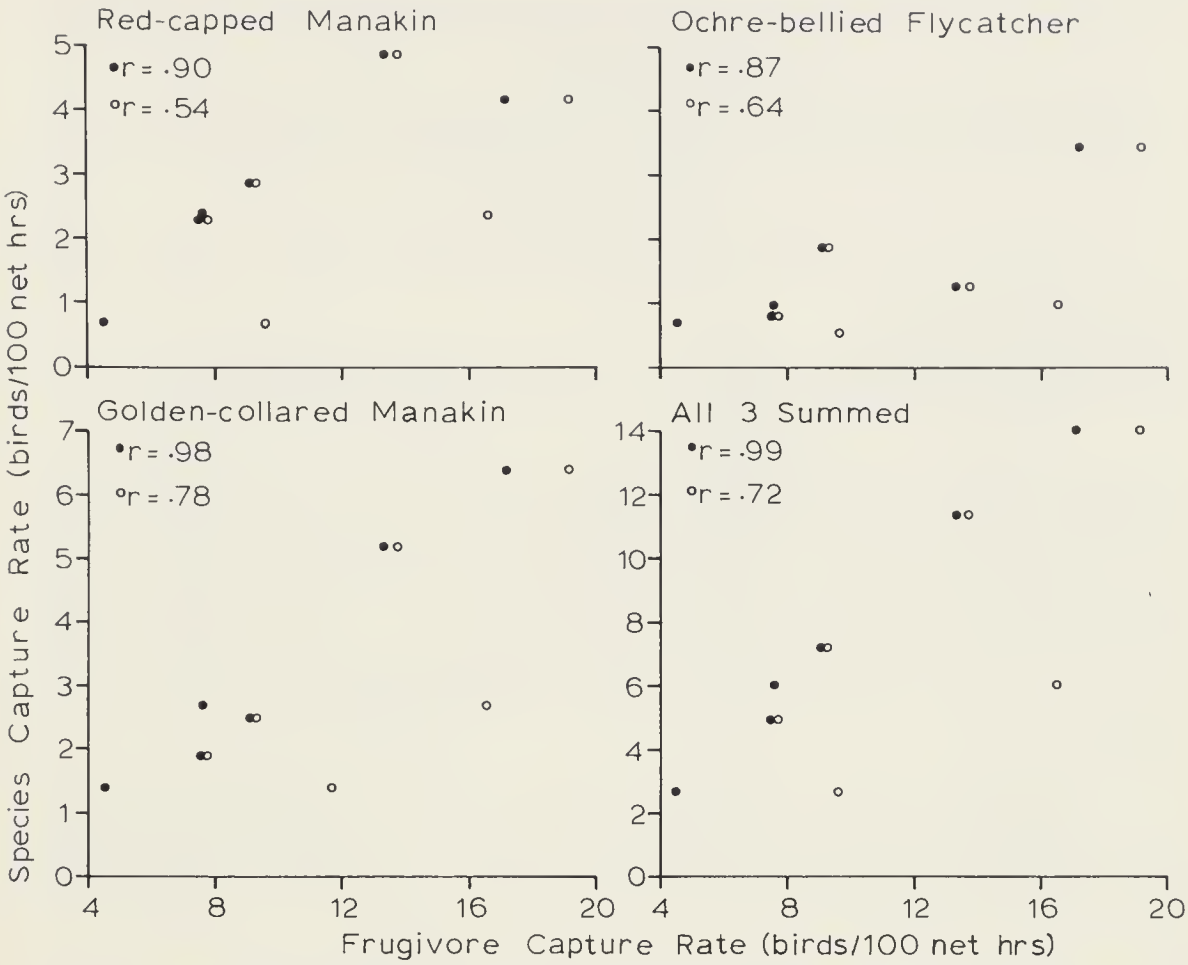


FIG. 4. Capture rate of the three most common frugivore species and the summed capture rate of all three species relative to the capture rate of all (migrants plus nonmigrants; open circles) and nonmigrant frugivores only (closed circles) for 200-bird samples. All comparisons with nonmigrant frugivores were significant and all comparisons with all frugivores were not significant.

that moved from the area of the original lines. Many IOFs, but no males, were recaptured on these new lines in late January (Table 5). This trend does not reflect net avoidance by IOFs because many (42%) IOFs were recaptured on these same lines in early March (Table 5). In general, however, IOFs had low recaptures. Thus, IOFs were much more transient than adult males.

The frequency of IOF Golden-collared Manakins (Table 5) tended to increase ($r = 0.83$, $P < 0.10$) with capture rates (Table 3) indicating that increased capture rates were the result of influxes of transient IOFs. Clearly, the increased capture rate in early March 1981 was due to influx of IOFs; 93% of the adult males captured in early March were recaptures, while only 42% of the IOFs were recaptures and 93% of the new (unbanded) individuals were IOFs (Table 5).

Finally, capture rates of adult males and IOFs showed males were less

TABLE 3

CAPTURE RATES (BIRDS/100 NET H) OF THE THREE MOST ABUNDANT FRUGIVORES

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early January | Late March | Early January | Late January | Early March | Late March |
| Red-capped Manakin | 4.2 | 2.4 | 2.3 | 2.9 | 4.9 | 0.7 |
| Golden-collared Manakin | 6.4 | 2.7 | 1.9 | 2.5 | 5.2 | 1.4 |
| Ochre-bellied Flycatcher | 3.5 | 1.0 | 0.8 | 1.9 | 1.3 | 0.6 |

transient than IOFs and that increased capture rates were due to the influx of IOFs. Capture rates for adult males in January 1980 (1.0 birds/100 net h), January 1981 (0.9) and early March 1981 (1.7) varied little. Capture rates for IOFs in January 1980 (5.4), January 1981 (1.0), and early March 1981 (3.5), however, varied by half an order of magnitude and paralleled changes in the overall capture rates of Golden-collared Manakins (Table 3).

*Red-capped Manakin.*—A total of 165 Red-capped Manakins was captured. Frequency of IOF Red-capped Manakins (Table 5) also increased ($r = 0.93$, $P < 0.01$) with capture rates (Table 3). Captures were generally skewed towards IOFs during all periods except early January 1981. The

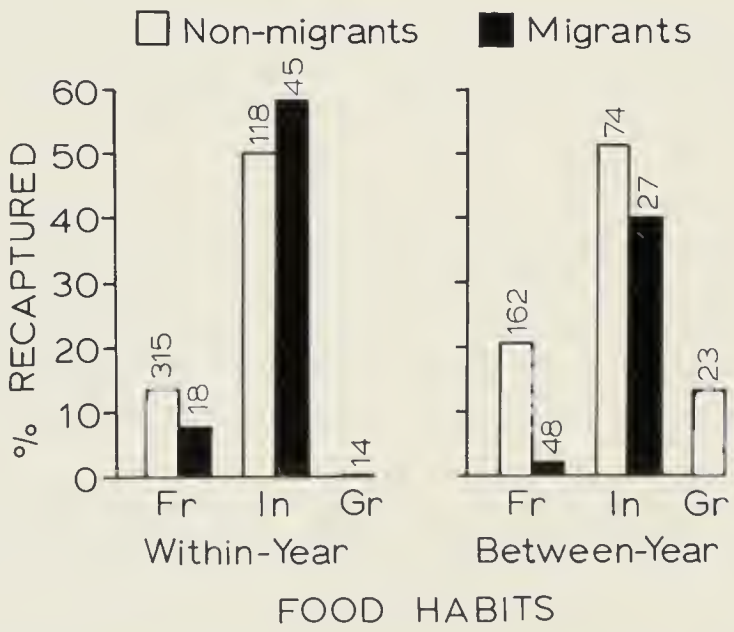


FIG. 5. Percent of individuals that were banded in January and recaptured in March (within-year) and banded in 1980 and recaptured in 1981 (between-year) for three guilds. Within-year recapture rates represent the average of 1980 and 1981. Numbers indicate the number of individuals originally banded. Guilds include frugivores (Fr), insectivores (In), and granivores (Gr).

TABLE 4

PERCENTAGE OF BANDED INDIVIDUALS (NUMBER BANDED) THAT WERE RECAPTURED BETWEEN MONTHS WITHIN A YEAR FOR BOTH YEARS AND THE PERCENTAGE RECAPTURED BETWEEN YEARS

| | Within years | Between years |
|---|---|---|
| Insectivores | | |
| Gray-headed Tanager | 0 (5) | 40 (5) |
| Plain-brown Woodcreeper | 0 (6) | 50 (2) |
| Spotted Antbird | 18 (11) | 33 (3) |
| Northern Royal Flycatcher | 40 (10) | 100 (5) |
| Plain Xenops | 42 (12) | 40 (10) |
| Slaty Antshrike | 42 (12) | 38 (13) |
| Chestnut-sided Warbler | 43 (7) | 25 (4) |
| Ovenbird | 44 (9) | 50 (10) |
| Southern Bentbill | 46 (13) | 57 (7) |
| Checker-throated Antwren | 50 (6) | — |
| White-flanked Antwren | 50 (6) | — |
| Ruddy-tailed Flycatcher | 50 (10) | 50 (4) |
| Buff-throated Woodcreeper | 73 (11) | 60 (10) |
| Dusky Antbird | 75 (16) | 67 (15) |
| Kentucky Warbler | 75 (24) | 80 (10) |
| Magnolia Warbler | 80 (5) | 66 (3) |
| Frugivores | | |
| Blue-crowned Manakin | 0 (6) | 50 (2) |
| Wood Thrush | 0 (8) | 13 (16) |
| Gray Catbird | 0 (5) | 0 (12) |
| Fulvous-vented Euphonia | 0 (14) | 0 (6) |
| Crimson-backed Tanager | 0 (5) | 50 (4) |
| Red-capped Manakin | 9 (99) | 6 (51) |
| Ochre-bellied Flycatcher | 14 (66) | 27 (26) |
| Swainson's Thrush | 20 (5) | 0 (21) |
| Red-throated Ant-tanager | 27 (22) | 50 (14) |
| Blue-black Grosbeak | 33 (6) | 0 (3) |
| Thrush-like Manakin | 43 (7) | 33 (3) |
| Golden-collared Manakin | 46 (90) | 38 (53) |

increased incidence of males in January 1981 can be attributed to the reduced abundance of IOFs rather than to an actual increase in males. No Red-capped Manakin lek was present on our study area, and both males and IOFs were transient; few individuals of either class were recaptured (Table 5). The number of transient males, however, was low and did not vary with the overall capture rates of Red-capped Manakins (capture rates of adult males were 0.4, 0.9, 0.3 birds/100 net h for January 1980, January 1981, and early March 1981, respectively). On the other hand, presence

TABLE 5

NUMBER OF GOLDEN-COLLARED AND RED-CAPPED MANAKINS CAPTURED IN EACH NETTING PERIOD, PERCENT OF CAPTURES THAT WERE RECAPTURES, PERCENT OF JANUARY-BANDED BIRDS THAT WERE RECAPTURED IN MARCH, AND THE PERCENT OF BIRDS BANDED IN 1980 THAT WERE RECAPTURED IN 1981

| | January | | | | March | | | |
|---|---|---|---|---|---|---|---|---|
| | Early | | Late | | Early | | Late | |
| | IOF[a] | Males | IOF | Males | IOF | Males | IOF | Males |
| Golden-collared Manakins | | | | | | | | |
| Number captured | 33/11[b] | 7/7 | —/18 | —/14 | —/26 | —/15 | 18/10 | 3/2 |
| % captures that were recaptures | —/18 | —/71 | —/22 | —/0 | —/42 | —/93 | 28/30 | 100/100 |
| % January recaptures | | | | | | | 15/22 | 43/76 |
| % 1980 recaptures | | | | | | | 33 | 71 |
| Red-capped Manakins | | | | | | | | |
| Number captured | 30/14 | 3/17 | —/26 | —/10 | —/37 | —/3 | 18/7 | 0/0 |
| % captures that were recaptures | —/0 | —/0 | —/4 | —/0 | —/24 | —/0 | 0/14 | 0/0 |
| % January recaptures | | | | | | | 0/6 | 0/0 |
| % 1980 recaptures | | | | | | | 6 | 0 |

[a] Immature or female.
[b] 1980/1981.

of IOFs was variable (capture rates of 3.8, 1.4, and 4.6 birds/100 net h in January 1980, January 1981, and early March 1981, respectively), paralleling changes in overall capture rates of Red-capped Manakins (Tables 3, 5). Thus, variation in capture rates of Manakins reflected presence or absence of transient IOFs and, in general, mirrored variation in capture rates of nonmigrant frugivores (Fig. 4).

## DISCUSSION

*Transience and fluctuations in capture rates.*—Guild patterns may not necessarily apply to all species within a guild; species within a guild may differ in their transience (e.g., see Table 4, also Faaborg et al. 1984). An analysis of individual species is inappropriate with the present data due to the rarity of most of the species. Analyses of guilds, however, as performed here, identify central guild tendencies in spatial stability that provide a basis for more specific tests of individual species in future studies.

Insect foods are thought to be less patchy in space and time than nectar or fruits (Karr 1976a), so that spatial stability (territoriality) is most profitable for insectivores (Horn 1968). Indeed, insectivores exhibited the greatest recapture rates (Fig. 5) (Table 4). Spatial stability could not be directly analyzed for nectarivores because they were not banded.

Frugivores were the most variable of the guilds, and they provided evidence that such variability can be due, in part, to movements. The increase in frugivores during 1981 could not have been due to recruitment because the sampling periods were prior to the main nesting season and after the period of juvenile dispersal of manakins (Worthington 1982). Moreover, the decline in frugivores in late March was too rapid and too severe to represent mortality; frugivore capture rates in late March were only one-third of their capture rates in early March (Fig. 3). Finally, the manakins provided the clearest evidence that movements were an important influence on variation in capture rates. The results showed that IOF manakins tended to be highly transient, while adult males were stable spatially. These results follow from the fact that adult males retain courtship arenas, while females and immatures are not restricted to any particular site or individual during the nonbreeding season (Chapman 1935, Skutch 1949, Snow 1962a, b). The association between presence of transient IOF manakins and capture rates, plus the high frequency of recaptures between sets of lines document that movements by transients account in part for temporal changes in abundances of frugivores within a locality.

Such transience may reflect movements in response to lek locations or, alternatively, food availability. January 1981 was the wettest on record

(57 years of data); heavy rain in the early dry season delayed fruiting. In addition, the dry season of 1980 was wetter than average (Table 1), and a wet dry season tends to create fruit failure in the following year (Foster 1982). Capture rates of frugivores were indeed lower in January 1981 as compared to 1980. Even migrant frugivores such as Bay-breasted Warblers, Gray Catbirds, and Wood Thrushes that were commonly seen and netted in January 1980 were not seen or captured in January 1981 (Appendix 1). This decrease in January 1981 can not simply reflect mortality because abundances increased during the dry season in 1981 to the point where capture rates in early March 1981 equalled capture rates in January of 1980 (Fig. 3). In short, variable capture rates can be due to movement in addition to the normal population processes of recruitment and mortality.

*Decline in frugivores in late March.*—One possible explanation for the decrease in frugivore captures on our young forest site in late March is sampling artifact; birds may simply learn (from being captured in January) to avoid nets in March (Terborgh and Weske 1969; Karr 1977, 1979, 1981b). Several lines of evidence, however, argue against this possibility. First, capture rates of the three most common frugivore species in nearby old forest, which included Red-capped Manakins and Ochre-bellied Flycatchers, increased in late March relative to January (J. R. Karr, unpubl. data). Second, mist-net lines that were operated in late January and early March provided less time between sampling periods for birds to "forget" net locations than on the lines operated in early January and late March. Yet, capture rates of frugivores increased in early March relative to late January, while capture rates declined in late March of both years. Moreover, recapture rates of both manakin species were very high in early March (Table 5), which also indicates a lack of net avoidance. Third, all guilds did not show a decline from January to late March; nectarivores and insectivores increased or remained stable in both years. It is unlikely that frugivores decreased simply because frugivores were better at avoiding nets than the other groups. Fourth, birds did not move above net level in late March. The canopy was only 5 m high on the lines sampled in late March (Fig. 1), so birds had little space to move above nets. Furthermore, nonmigrant abundance at canopy fruits was extremely low in late March (Martin 1982, 1985a). Thus, net avoidance did not cause the seasonal patterns and the decrease in frugivores in late March.

The decrease in nonmigrant frugivores in late March could have been influenced by the influx of migrating frugivores; nonmigrants decreased in both years at a time when migrants appeared in large numbers and food was increasing (Smythe 1970, Croat 1978). Food sources of nectarivores also increase in the late dry season (Croat 1978), and nectarivores, which include few to no migrants, did not decrease in late March.

Alternatively, the temporal dynamics may reflect differential availability of food in different habitats. Frugivores should select and switch among habitats and patches as a function of fruit quality and abundance relative to other environmental influences such as predation risk or competition (Martin 1985b, Martin and Karr 1986). Bird-dispersed fruit plants are denser in young than old forest (Martin 1985a, unpubl. data) and fruit abundance appears to be lowest in December through February in older forest (Foster 1973, 1980, 1982). Some old forest frugivores may switch to young forest during this period and then switch back to old forest in the late dry season when fruits become more abundant. The increase in capture rates of Red-capped Manakins and Ochre-bellied Flycatchers in old forest in late March (J. R. Karr, unpubl. data) when they decline in young forest suggests possible habitat switching.

Some frugivores may move to our site from wetter or drier areas during the dry season; a marked moisture gradient exists over a short distance across the Isthmus of Panama (Rand and Rand 1982), and Karr and Freemark (1983) have provided evidence for the importance of macro- and microclimate for bird movements. The actual answer may lie in some combination of all these factors. Whatever the reason, transients apparently form a significant component of tropical bird communities, and the basis for their movements and their impact on residents needs investigation if we are ever to preserve the necessary habitats to sustain their populations.

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## Appendix 1

Bird Species Captured in 200-bird Samples or Detected in a Second-growth Woodland in Panama

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early Jan. | Late Mar. | Early Jan. | Late Jan. | Early Mar. | Late Mar. |
| Little Tinamou (*Crypturellus soui*) (G)[a] | +[b] | 1 | + | + | + | 1 |
| Broad-winged Hawk (*Buteo platypterus*)[c] | – | + | – | – | – | 1 |
| Collared Forest-Falcon (*Micrastur semitorquatus*) | – | + | – | – | – | – |
| Gray-headed Chachalaca (*Ortalis cinereiceps*) | + | + | + | + | + | + |
| Scaled Pigeon (*Columba speciosa*) | – | – | – | + | + | – |
| Blue Ground-Dove (*Claravis pretiosa*) (F) | – | 3 | + | + | + | 1 |
| White-tipped Dove (*Leptotila verreauxi*) | – | + | – | – | – | + |
| Gray-chested Dove (*L. cassinii*) (F) | – | + | 1 | 2 | – | 4 |
| Orange-chinned Parakeet (*Brotogeris jugularis*) | + | – | + | + | – | – |
| Blue-headed Parrot (*Pionus menstruus*) | + | – | + | + | – | – |
| Red-lored Parrot (*Amazona autumnalis*) | + | + | + | – | – | – |
| Squirrel Cuckoo (*Piaya cayana*) | – | + | – | – | + | + |
| Pheasant Cuckoo (*Dromococcyx phasianellus*) (I) | – | 1 | – | + | + | 1 |
| Common Pauraque (*Nyctidromus albicollis*) (I) | – | 1 | + | + | + | + |
| Rufous-breasted Hermit (*Glaucis hirsuta*) (N) | 1 | + | – | 1 | – | + |
| Long-tailed Hermit (*Phaethornis superciliosus*) (N) | 2 | 9 | 10 | 9 | 10 | 24 |
| Little Hermit (*P. longuemareus*) (N) | 5 | 2 | 5 | 2 | 1 | 1 |
| White-necked Jacobin (*Florisuga mellivora*) (N) | 1 | 2 | 1 | – | 1 | + |
| Violet-bellied Hummingbird (*Damophila julie*) (N) | 8 | 9 | 3 | 9 | 4 | 5 |
| Blue-chested Hummingbird (*Amazilia amabilis*) (N) | 1 | 3 | 7 | 7 | 2 | 13 |
| Snowy-bellied Hummingbird (*A. edward*) (N) | 1 | – | – | – | – | – |
| Rufous-tailed Hummingbird (*A. tzacatl*) (N) | 1 | 6 | 4 | + | 2 | 1 |
| White-vented Plumeleteer (*Chalybura buffonii*) (N) | – | – | – | + | 2 | – |
| White-tailed Trogon (*Trogon viridis*) | + | + | + | – | + | – |
| Violaceous Trogon (*T. violaceus*) (F) | + | – | 1 | + | – | – |
| Slaty-tailed Trogon (*T. massena*) (F) | – | – | 1 | + | – | – |

## Appendix 1
Continued

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early Jan. | Late Mar. | Early Jan. | Late Jan. | Early Mar. | Late Mar. |
| Blue-crowned Motmot (*Momotus momota*) (F) | + | 1 | 2 | 1 | 1 | 1 |
| Rufous Motmot (*Baryphthengus ruficapillus*) (F) | – | – | – | – | 1 | – |
| American Pygmy Kingfisher (*Chloroceryle aenea*) (P) | – | 1 | – | – | – | – |
| White-necked Puffbird (*Bucco macrorhynchus*) | – | – | + | + | – | – |
| Collared Aracari (*Pteroglossus torquatus*) (F) | + | + | + | + | + | 2 |
| Keel-billed Toucan (*Rhamphastos sulfuratus*) | + | + | + | + | + | + |
| Black-cheeked Woodpecker (*Melanerpes pucherani*) | – | + | – | – | + | – |
| Lineated Woodpecker (*Dryocopus lineatus*) | – | + | – | – | + | + |
| Buff-throated Foliage-gleaner (*Automolus ochrolaemus*) (I) | – | – | 2 | 1 | + | – |
| Plain Xenops (*Xenops minutus*) (I) | 3 | 3 | 2 | 3 | 4 | 3 |
| Scaly-throated Leaftosser (*Sclerurus guatemalensis*) (I) | – | – | 2 | 2 | 1 | – |
| Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) (I) | 2 | – | 1 | 3 | – | 1 |
| Ruddy Woodcreeper (*D. homochroa*) (I) | – | – | 1 | – | – | – |
| Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) (I) | – | – | 1 | + | – | – |
| Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) (I) | 3 | 5 | 2 | 6 | 2 | 1 |
| Fasciated Antshrike (*Cymbilaimus lineatus*) (I) | – | 1 | – | – | + | + |
| Slaty Antshrike (*Thamnophilus punctatus*) (I) | 6 | 4 | 6 | 6 | 4 | 6 |
| Checker-throated Antwren (*Myrmotherula fulviventris* (I) | – | 1 | 2 | 4 | 2 | + |
| White-flanked Antwren (*M. axillaris*) (I) | – | + | 5 | – | 4 | + |
| Dot-winged Antwren (*Microrhopias quixensis*) | – | + | + | – | + | – |
| Dusky Antbird (*Cercomacra tyrannina*) (I) | 4 | 6 | 5 | 2 | 3 | 4 |
| White-bellied Antbird (*Myrmeciza longipes*) (I) | – | 1 | – | 1 | – | – |
| Chestnut-backed Antbird (*M. exsul*) | – | – | – | – | + | – |
| Spotted Antbird (*Hylophylax naevioides*) (I) | 3 | – | 3 | 6 | 6 | 2 |
| Bicolored Antbird (*Gymnopithys leucaspis*) (I) | – | + | 3 | 3 | 2 | + |
| Ocellated Antbird (*Phaenostictus mcleannani*) (I) | 1 | – | + | 1 | 2 | 2 |

## Appendix 1
Continued

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early Jan. | Late Mar. | Early Jan. | Late Jan. | Early Mar. | Late Mar. |
| Black-faced Antthrush (*Formicarius analis*) (I) | – | – | + | 1 | + | – |
| Ochre-bellied Flycatcher (*Mionectes oleagineus*) (F) | 22 | 6 | 10 | 20 | 11 | 6 |
| Southern Bentbill (*Oncostoma olivaceum*) (I) | 5 | 5 | 2 | 6 | 5 | 4 |
| Brownish Flycatcher (*Cnipodectes subbrunneus*) (I) | – | – | 1 | 3 | 1 | 1 |
| Olivaceous Flatbill (*Rhynchocyclus olivaceus*) (I) | – | – | – | 3 | – | – |
| Golden-crowned Spadebill (*Platyrinchus coronatus*) (I) | – | 1 | – | – | 3 | + |
| Northern Royal Flycatcher (*Onychorhynchus mexicanus*) (I) | 3 | 1 | 2 | 3 | + | 2 |
| Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*) (I) | 5 | 1 | 4 | 2 | 3 | 1 |
| Black-tailed Flycatcher (*Myiobius atricaudus*) (I) | 1 | 2 | – | – | + | – |
| Acadian Flycatcher (*Empidonax virescens*)[c] (I) | 1 | 2 | 1 | 2 | – | 1 |
| Willow Flycatcher (*E. traillii*)[c] (I) | – | 2 | – | – | – | – |
| Bright-rumped Attila (*Attila spadiceus*) (F) | – | – | 1 | 3 | 1 | + |
| Speckled Mourner (*Laniocera rufescens*) (F) | + | – | – | – | 1 | – |
| Rufous Mourner (*Rhytipterna holerythra*) | – | + | – | – | – | – |
| Dusky-capped Flycatcher (*Myiarchus tuberculifer*) (I) | + | 3 | – | – | 1 | 3 |
| Panama Flycatcher (*M. panamensis*) (F) | 1 | 1 | + | + | + | 1 |
| Great Crested Flycatcher (*M. crinitus*)[c] (F) | – | 1 | + | + | + | 1 |
| Boat-billed Flycatcher (*Megarhynchus pitangua*) | + | – | – | – | – | + |
| Social Flycatcher (*Myiozetetes similis*) | + | – | + | + | + | + |
| Streaked Flycatcher (*Myiodynastes maculatus*) | + | + | + | + | + | + |
| Tropical Kingbird (*Tyrannus melancholicus*) | – | + | – | + | + | + |
| Eastern Kingbird (*T. tyrannus*)[c] (F) | – | 1 | – | + | + | + |
| Masked Tityra (*Tityra semifasciata*) | – | – | – | + | + | – |
| Black-crowned Tityra (*T. inquisitor*) | – | + | – | + | + | – |
| Blue Cotinga (*Cotinga nattererii*) | + | + | + | + | + | + |
| Purple-throated Fruitcrow (*Querula purpurata*) | – | + | – | + | + | – |

## Appendix 1
Continued

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early Jan. | Late Mar. | Early Jan. | Late Jan. | Early Mar. | Late Mar. |
| Thrushlike Manakin (*Schiffornis turdinus*) (F) | 3 | 1 | 2 | 4 | 3 | 6 |
| Golden-collared Manakin (*Manacus vitellinus*) (F) | 38 | 17 | 23 | 26 | 43 | 14 |
| Blue-crowned Manakin (*Pipra coronata*) (F) | 1 | – | 3 | 2 | 2 | – |
| Red-capped Manakin (*P. mentalis* (F) | 25 | 15 | 27 | 30 | 41 | 7 |
| Black-bellied Wren (*Thryothorus fasciatoventris*) (I) | – | – | – | – | 1 | – |
| Bay Wren (*T. nigricapillus*) (I) | 1 | – | + | – | 3 | 1 |
| Plain Wren (*T. modestus*) (I) | – | – | 1 | – | – | – |
| White-breasted Wood-Wren (*Henichorina leucosticta*) (I) | 2 | – | – | 1 | 1 | – |
| Song Wren (*Cyphorhinus phaeocephalus*) (I) | 2 | – | 3 | 3 | 2 | 1 |
| Long-billed Gnatwren (*Ramphocaenus melanurus*) (I) | 1 | – | – | 1 | – | – |
| Tropical Gnatcatcher (*Polioptila plumbea*) | + | – | – | + | – | – |
| Swainson's Thrush (*Catharus ustulatus*)[c] (F) | 1 | 8 | 3 | – | 1 | 18 |
| Wood Thrush (*Hylocichla mustelina*)[c] (F) | 3 | 8 | – | 1 | 1 | 4 |
| Clay-colored Robin (*Turdus grayi*) (F) | + | – | + | + | 2 | + |
| Gray Catbird (*Dumetella carolinensis*)[c] (F) | 2 | 6 | – | – | – | + |
| Yellow-throated Vireo (*Vireo flavifrons*)[c] | – | + | – | – | – | – |
| Red-eyed Vireo (*V. olivaceus*)[c] | – | – | – | – | – | + |
| Yellow-green Vireo (*V. flavoviridis*) | – | – | – | – | + | – |
| Blue-winged Warbler (*Vermivora pinus*)[c] (I) | – | + | – | – | – | 1 |
| Golden-winged Warbler (*V. chrysoptera*)[c] | – | + | – | – | – | – |
| Tennessee Warbler (*V. peregrina*)[c] (F) | + | 23 | – | – | – | 24 |

## Appendix 1
Continued

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early Jan. | Late Mar. | Early Jan. | Late Jan. | Early Mar. | Late Mar. |
| Chestnut-sided Warbler (*Dendroica pensylvanica*)[c] (I) | + | 3 | 3 | 2 | + | 2 |
| Magnolia Warbler (*D. magnolia*)[c] (I) | 3 | 1 | 2 | 1 | 1 | + |
| Bay-breasted Warbler (*D. castanea*)[c] (F) | 3 | 6 | – | – | + | 1 |
| Black-and-white Warbler (*Mniotilta varia*)[c] (I) | – | 2 | – | – | – | – |
| Prothonotary Warbler (*Protonotaria citrea*)[c] (I) | – | + | – | – | – | 1 |
| Ovenbird (*Seiurus aurocapillus*)[c] (I) | 4 | 5 | 2 | 1 | – | 2 |
| Northern Waterthrush (*S. noveboracensis*)[c] (I) | – | – | – | 1 | – | – |
| Kentucky Warbler (*Oporornis formosus*)[c] (I) | 5 | 4 | 6 | 9 | 4 | 6 |
| Mourning Warbler (*O. philadelphia*)[c] (I) | – | 1 | + | – | – | – |
| Plain-colored Tanager (*Tangara inornata*) | + | + | + | + | + | + |
| Golden-masked Tanager (*T. larvata*) | + | + | – | + | + | – |
| Scarlet-thighed Dacnis (*Dacnis venusta*) | – | – | – | + | + | – |
| Blue Dacnis (*D. cayana*) (N) | – | + | + | + | + | 1 |
| Green Honeycreeper (*Chlorophanes spiza*) | + | – | – | + | – | + |
| Red-legged Honeycreeper (*Cyanerpes cyaneus*) (N) | 1 | 1 | – | 1 | + | 1 |
| Fulvous-vented Euphonia (*Euphonia fulvicrissa*) (F) | 3 | + | 8 | + | + | – |
| Blue-gray Tanager (*Thraupis episcopus*) | + | – | + | + | + | + |
| Gray-headed Tanager (*Eucometis penicillata*) (I) | 3 | + | – | 1 | 1 | 3 |
| White-shouldered Tanager (*Tachyphonus luctuosus*) (I) | + | – | 1 | + | – | 3 |
| White-lined Tanager (*T. rufus*) | – | + | – | – | – | – |
| Red-throated Ant-tanager (*Habia fuscicauda*) (F) | 8 | 3 | 8 | 5 | 6 | 6 |

## Appendix 1
Continued

| | 1980 | | 1981 | | | |
|---|---|---|---|---|---|---|
| | Early Jan. | Late Mar. | Early Jan. | Late Jan. | Early Mar. | Late Mar. |
| Summer Tanager (*Piranga rubra*)[c] (F) | – | 4 | – | – | 1 | 1 |
| Crimson-backed Tanager (*Ramphocelus dimidiatus*) (F) | 1 | 2 | 3 | + | 1 | 1 |
| Yellow-rumped Tanager (*R. icteronotus*) | – | + | + | + | + | + |
| Streaked Saltator (*Saltator albicollis*) (F) | + | 2 | – | – | – | 1 |
| Buff-throated Saltator (*S. maximus*) (F) | – | 1 | 2 | + | 1 | 1 |
| Rose-breasted Grosbeak (*Pheucticus ludovicianus*)[c] (F) | – | 1 | – | – | – | 3 |
| Blue-black Grosbeak (*Cyanocompsa cyanoides*) (F) | 2 | 1 | 3 | 1 | 4 | + |
| Indigo Bunting (*Passerina cyanea*)[c] (F) | 3 | – | – | – | – | – |
| Black-striped Sparrow (*Arremonops conirostris*) | + | – | + | + | + | + |
| Blue-black Grassquit (*Volatinia jacarina*) (G) | – | 1 | – | – | – | – |
| Variable Seedeater (*Sporophila aurita*) (G) | 3 | 4 | 7 | – | 1 | + |
| Thick-billed Seed-Finch (*Oryzoborus funereus*) (G) | 2 | 5 | 1 | – | + | + |
| Yellow-backed Oriole (*Icterus chrysater*) | + | – | + | + | – | – |
| Northern Oriole (*I. galbula*)[c] | + | + | – | + | – | + |
| Scarlet-rumped Cacique (*Cacicus uropygialis*) | – | + | + | + | + | + |
| Chestnut-headed Oropendola (*Psarocolius wagleri*) | – | – | + | – | + | – |

[a] Guild designations: I = insectivore, F = frugivore, N = nectarivore, G = granivore, P = piscivore. Guild designations are provided only for species captured in 200-bird samples.
[b] Number of captures, detection (+), or lack of detection (–).
[c] Migrants from North America.

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# STRUCTURE, SEASONAL DYNAMICS, AND HABITAT RELATIONSHIPS OF AVIAN COMMUNITIES IN SMALL EVEN-AGED FOREST STANDS

RICHARD H. YAHNER[1]

ABSTRACT.—Structure, stability, and habitat relationships of avian communities associated with small even-aged stands were studied for three consecutive winters and breeding seasons in aspen (*Populus* spp.) and mixed-oak (*Quercus* spp.) cover type in an area managed for Ruffed Grouse (*Bonasa umbellus*) habitat. Thirteen and 69 species were noted in six habitat types during winter and the breeding season, respectively. Trunk-bark foragers predominated in winter, particularly in uncut habitats; in contrast, the ground-shrub foraging guild predominated in the breeding season, especially in clearcut habitats. The six habitat types were segreated in two groups (uncut and clearcut) on the basis of the stability of the trunk-bark and ground-shrub foraging guilds in winter and the breeding season, respectively. Black-capped Chickadees (*Parus atricapillus*) in winter and Rufous-sided Towhees (*Pipilo erythrophthalmus*) in the breeding season were the most abundant species. Habitat variables describing overstory trees and snags were among those important to trunk-bark and sallier-canopy foraging guilds; variables describing shrub and understory vegetation were associated with the ground-shrub foraging guild. The habitat fragmentation created by the current cutting cycle has had no discernible negative impact on the avifauna, and species adapted to early-successional habitats have benefited. *Received 19 Apr. 1985, accepted 15 Aug. 1985.*

Habitat size and age are two major determinants of avian community structure in even-aged forest stands affected by clearcutting (e.g., Conner et al. 1979, Titterington et al. 1979, Crawford et al. 1981, Niemi and Hanowski 1984). If size of even-aged forest stands were held constant, but age were allowed to vary, then researchers could obtain better insight into the effects of vegetative complexity, which often is a function of age since clearcutting (e.g., Yahner and Grimm 1984), on avifauna. A long-term management study for Ruffed Grouse (*Bonasa umbellus*) habitat consisting of a patchwork of one-ha even-aged stands in aspen (*Populus* spp.) and mixed-oak (*Quercus* spp.) cover types in central Pennsylvania (Liscinsky 1980) provided a unique opportunity to address two objectives: (1) to compare structure and seasonal dynamics of wintering and breeding avian communities among small even-aged stands of different age and cover type, and (2) to examine avian-habitat relationships in these small stands. General trends in avian abundance patterns between a large unmanaged sector and a large managed sector of the study area affected by

[1] Forest Resources Lab., School of Forest Resources, The Pennsylvania State Univ., University Park, Pennsylvania 16802.

the Ruffed Grouse management plan were investigated previously (Yahner 1984).

## STUDY AREA

The study was conducted at the Barrens Grouse Habitat Management Study Area (BGMA), State Game Lands 176, Centre County, Pennsylvania, from December 1981 to June 1984. Major canopy trees on the study area include white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and pitch pine (*Pinus rigida*). Principal understory and shrub species are scrub oak (*Q. ilicifolia*), dwarf chinkapin oak (*Q. muehlenbergii*), aspen, red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and blueberry (*Vaccinium* spp.). Aspen cover is adjacent to an unimproved dirt road that bisects the BGMA in a northeast-southwest direction, whereas the mixed-oak cover type is about 400 m away from each side of the road. No streams or lakes occur at the BGMA, but a few temporary ponds are present.

The 1166 ha BGMA is divided into a control (unmanaged) and a treated (managed) sector of equal size. The treated sector is comprised of 136, 4-ha square blocks, each representing "activity centers" for Ruffed Grouse under the supervision of the Pennsylvania Game Commission. Sixty and 76 blocks are in aspen and mixed-oak cover types, respectively. A block is divided into four one-ha stands (100 × 100 m). The western stand in all blocks was cut in the winter 1976–77, and the northern stand in aspen blocks was cut only in the winter of 1980–81. Thus, aspen stands of three age classes and mixed-oak stands of two age classes are present on the treated sector, with 36% of this sector affected by clearcutting. The forest on the control sector and uncut stands on the treated sector are about 60 years old.

A total of 18 ha in six habitat "types" was selected for study. Types were distinguished on the basis of distance from clearcutting, age since clearcutting, and cover type. These included three one-ha stands on the control sector (hereafter termed control habitat), plus three one-ha stands each in uncut aspen (mature aspen habitat), western aspen (1976–77 aspen habitat), northern aspen (1980–81 aspen habitat), uncut mixed-oak (mature oak habitat), and western mixed-oak stands (1976–77 oak habitat) on the treated sector. Stands selected were representative of vegetative features and were >50 m from habitat disturbances created by the unimproved dirt road, restricted access roads, corridors along transmission powerlines, or frost pockets (additional details of each habitat type are presented in Yahner 1983a).

## METHODS

*Habitat sampling techniques.*—Four random, 0.04-ha circular samples (James and Shugart 1970) were established in each one-ha stand for measurement of habitat variables in spring and summer 1982, of which two plots each were in a central and an edge zone (Yahner and Grimm 1984). The central zone was the 50 × 50 m interior portion of a stand, and the edge zone was the remaining 25–m wide border surrounding the central zone (after Strelke and Dickson 1980). Overstory tree (woody stem > 1.5 m tall, >7.5 cm dbh) variables included number of species and density (no./ha) and basal area ($m^2$/ha) of each species, of snags, and of all species and snags combined in the 0.04–ha sample. Understory tree (woody stem ≥ 1.5 m tall, 2.5–7.5 cm dbh) variables were number of species and density (no./ha) of each species and of all species combined in the 0.04-ha sample. Tall shrub (woody stem ≥ 1.5 m tall, <2.5 cm dbh) and short shrub (woody stem = 0.5–1.5 m tall, <2.5 cm dbh) variables were number of species and density (no./ha) of each species and of all species combined in

two perpendicular, one-m wide transects in the 0.04-ha sample. Percent coverages of canopy, grasses and sedges combined, forbs, and total vegetation (grass, sedge, forb, and woody vegetation) at one m above ground were measured by taking 20 ocular tube sightings spaced at 2-m intervals along the transects. Growth-form diversity also was determined at the 20 sightings. This diversity was based on the presence of four growth forms (overstory trees, understory trees, short-tall shrubs, and herbs) and the Shannon index $H' = -\sum p_i \ln p_i$, where $p_i$ is the proportion of sightings containing the $i$th growth form. Density (no./ha) of stumps (>0.25 m tall, >7.5 cm in diameter) and total length (m) of fallen logs (>3 cm in diameter) also were noted in each 0.04-ha sample. (Sampling methods, details of variables, and significant differences in variables among habitat types are given in Yahner and Grimm 1984.)

*Avian sampling techniques.*—Ten avian censuses were conducted each winter (late December–early March) and breeding season (late April–late June) for 3 consecutive years, giving 30 censuses per season in each habitat type. Censuses were conducted approximately once weekly; a similar census schedule was followed each year. All habitat types were censused on the same day (sunrise–10:30), and the order in which individual stands were visited per census was randomized. All birds seen or heard were recorded by observers who walked slowly along two 100-m transects spaced 50 m apart in each stand. Birds entering or leaving a stand were noted, but birds flying over the canopy were excluded (Conner and Dickson 1980).

Mean species richness ($S$), species diversity ($H'$), and total density were calculated per season in the six habitat types for all species combined and for three major foraging guilds, based on 30 censuses pooled over the three years. Combining data for each habitat type gave a better measure of avian habitat-use patterns and also increased sample size for statistical analyses compared to examining data from individual years (Rice et al. 1984). $S$ is the total number of species; $H'$ is based on the Shannon index, where $p_i$ is the proportion of individuals of the $i$th species; and total density is the total number of individuals (no./10 ha) of all species combined. Major guilds were ground-shrub foragers (species typically foraging at ground level or <2 m above ground in vegetation), trunk-bark foragers (species typically foraging along main tree trunks or large branches), and sallier-canopy foragers (species typically foraging ≥2 m above ground in vegetation) (modified from Holmes et al. 1979, Swift et al. 1984). Mean density (no./10 ha) of individual species was determined per season in each habitat type. In addition, an importance value ($IV$) was derived for each major foraging guild and species per season in each habitat type (Kricher 1973, Yahner 1983b). An $IV$ was the proportion of total censuses in which a foraging guild (or species) was recorded per season in a habitat type (×100) plus the relative mean total density (or mean species density) of a foraging guild (or species) per season in habitat type (×100) (maximum $IV = 200$); a foraging guild or species with an $IV \geq 75$ in either winter or the breeding season arbitrarily was classified as being an important component of the avian community in a given habitat type. The number of territories per foraging guild and species in each habitat type was determined during the breeding season using the spot-mapping technique (Williams 1936). A minimum of three contacts of a singing male was used to delineate territorial boundaries (IBCC 1970); partial territories (<50% with an individual stand) were estimated to the nearest 10%.

Mean $S$, $H'$, and total density for all species combined and for each major foraging guild, as well as mean density for each common species (≥30 contacts in a given season), were compared among the six habitat types during winter and the breeding season using single-classification analyses of variance (ANOVA) and Kruskal-Wallis tests; a posteriori comparisons between habitat types were made with Student-Newman-Keuls and STP tests (Sokal and Rohlf 1981).

The six habitat types and 88 avian variables were considered as columns and rows, respectively, of a data matrix. Avian variables included mean and coefficient of variation (CV) of $S$, $H'$, and total density for all species combined and for each foraging guild; mean and CV of density for each common species in winter and the breeding season; cumulative numbers of all species combined and species per foraging guild in both winter and the breeding season; and cumulative number of territories for all species combined, each foraging guild, and each common species. These data were analyzed by $Q$-factor analysis (BMDP4M, Dixon 1981) to show associations among the six habitat types based on all avian population and community variables (after Yahner 1983b). A varimax (orthogonal) rotation was used, and factors were extracted by eigenvalues exceeding 0.5 (Rummel 1970).

Relationships between habitat variables and avian variables were analyzed with simple correlation analyses because of small sample size (N = six habitat types) and multicollinearity among habitat variables (after Dueser and Brown 1980, Yahner 1983b). If necessary, log-transformed data were used in correlation analyses to meet assumptions of the test (Sokal and Rohlf 1981).

## RESULTS

*Winter community structure.*—The cumulative number of species per habitat type ranged from 1 to 9 during winter (Table 1). Mean $S$, $H'$, and total density for all species combined and for the trunk-bark foraging guild were higher in the three uncut than in the three clearcut habitats. The $IV$ of the trunk-bark foraging guild exceeded 150 in each uncut habitat. Conversely, the ground-shrub foraging guild was poorly represented ($IV \leq 51$) in all habitat types, and no sallier- or canopy-foraging species were noted.

Of 13 wintering species (scientific names in Table 4) recorded in the six habitat types, only Black-capped Chickadees, Downy Woodpeckers, and White-breasted Nuthatches were common species (Table 2). These three species of trunk-bark foragers typically had a high $IV$ in uncut habitats. Black-capped Chickadees were noted in all habitat types, and Downy Woodpeckers and White-breasted Nuthatches were absent only from 1980–81 aspen.

*Breeding community structure.*—The cumulative number of species observed per habitat types was much higher in the breeding season than in winter (Table 3). Mean $S$ and $H'$ for all species combined and for both the trunk-bark and sallier-canopy foraging guilds were generally highest in 1976–77 aspen and in uncut habitats. Mean total density and $IV$ of trunk-bark and sallier-canopy foraging guilds were higher in the three uncut habitats compared to the three clearcut habitats. Conversely, mean $S$ and total density for ground-shrub foragers were highest in 1976–77 aspen or 1976–77 oak habitats, or both. The $IV$ of the ground-shrub foraging guild exceeded those of other guilds in all six habitat types.

Sixteen of the 69 species observed in the six habitat types during the breeding season were considered common species (Table 4). Rufous-sided

TABLE 1

CUMULATIVE NUMBER OF SPECIES, MEANS ± SD OF WINTER AVIAN COMMUNITY VARIABLES, AND IMPORTANCE VALUES OF GUILDS IN SIX HABITATS AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE WINTERS (1982–84)

| Variable | Habitat type | | | | | |
|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak |
| Cumulative no. species: | | | | | | |
| All species combined | 7 | 8 | 8[a] | 1 | 9 | 5 |
| Ground-shrub forager | 1 | 3 | 3 | 0 | 1 | 1 |
| Trunk-bark forager | 6 | 5 | 4 | 1 | 8 | 4 |
| Species richness ($S$): | | | | | | |
| All species combined[b] | 1.8 ± 1.3† | 1.2 ± 1.2†* | 0.5 ± 0.7* | 0.1 ± 0.2 | 1.3 ± 1.4† | 0.6 ± 0.9* |
| Ground-shrub forager | 0.1 ± 0.2 | 0.2 ± 0.5 | 0.1 ± 0.4 | 0.0 ± 0.0 | 0.1 ± 0.3 | 0.3 ± 2.8 |
| Trunk-bark forager[b] | 1.8 ± 1.2† | 1.0 ± 1.0†*+ | 0.3 ± 0.7+§ | 0.1 ± 0.2§ | 1.2 ± 1.3†* | 0.5 ± 0.8*+ |
| Species diversity ($H'$): | | | | | | |
| All species combined[b] | 0.5 ± 0.5† | 0.3 ± 0.4†* | 0.1 ± 0.2*+ | 0.0 ± 0.0+ | 0.3 ± 0.4†* | 0.1 ± 0.3*+ |
| Trunk-bark forager[b] | 0.5 ± 0.5† | 0.2 ± 0.3†* | 0.1 ± 0.2+ | 0.0 ± 0.0+ | 0.3 ± 0.4† | 0.1 ± 0.2*+ |
| Total density (no./10 ha): | | | | | | |
| All species combined[b] | 10.3 ± 11.2† | 8.4 ± 9.8†* | 2.2 ± 3.9*+ | 0.2 ± 1.2+ | 8.2 ± 11.1†* | 3.3 ± 5.4* |
| Ground-shrub forager | 0.1 ± 0.6 | 1.0 ± 2.7 | 0.8 ± 2.3 | 0.0 ± 0.0 | 0.4 ± 1.7 | 0.6 ± 1.0 |
| Trunk-bark forager[b] | 9.8 ± 9.0† | 7.4 ± 9.1†* | 1.9 ± 4.0+§ | 0.2 ± 1.2§ | 7.8 ± 11.0†* | 2.7 ± 5.2*+ |
| Importance value, $IV$:[c] | | | | | | |
| Ground-shrub forager | 23 | 51 | 44 | 0 | 23 | 32 |
| Trunk-bark forager | 200 | 155 | 48 | 7 | 159 | 58 |

[a] Includes one sighting of a Red-tailed Hawk (*Buteo jamaicensis*).

[b] Significant difference among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.

[c] $IV$ based on the sum of the proportion of total censuses (×100) in which a guild was present in a given habitat type (maximum = 24 censuses for trunk-bark foragers in control) and the relative density of a guild in a given habitat type (maximum density = 9.77/10 ha for trunk-bark foragers in control); maximum value of $IV$ = 200.

TABLE 2

MEAN (± SD), DENSITY (NO./10 HA), AND IMPORTANCE VALUES FOR THREE SPECIES IN SIX HABITAT TYPES AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE WINTERS (1982–1984)

| Species | Habitat type | | | | | |
|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak |
| Downy Woodpecker[a] | 2.3 ± 2.5† (147)[b] | 1.4 ± 2.4†* (82) | 0.2 ± 0.8*+ (16) | 0.0 ± 0.0 (0) | 2.9 ± 3.8† (140) | 0.1 ± 0.6*+ (8) |
| Black-capped Chickadee | 4.3 ± 6.0†* (181) | 5.0 ± 6.5† (188) | 1.4 ± 3.4*+ (64) | 0.2 ± 1.2+ (10) | 3.3 ± 7.1†*+ (114) | 1.6 ± 3.6*+ (66) |
| White-breasted Nuthatch | 1.9 ± 2.6† (114) | 0.7 ± 1.8†* (37) | 0.1 ± 0.6* (8) | 0.0 ± 0.0* (0) | 0.6 ± 1.3†* (40) | 0.1 ± 0.6* (8) |

[a] Density of each species was significantly different among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.

[b] Importance values (*IV*) are based on the sum of the proportion of total censuses (×100) in which a species was present in a given habitat type (maximum = 17 censuses for Downy Woodpecker in control) and the relative density of a species in a given habitat type (maximum density = 5.00/10 ha for Black-capped Chickadee in mature aspen); maximum *IV* = 200.

Towhees predominated (high density and *IV*) in all habitat types except 1980–81 aspen. Ovenbirds and Black-and-white Warblers seldom occurred in clearcut habitats. In contrast, Common Yellowthroats and Field Sparrows were characteristic of all three clearcut habitats. Gray Catbirds, Golden-winged Warblers, and Chestnut-sided Warblers were abundant in only older clearcut habitats, i.e., 1976–77 aspen and 1976–77 oak.

*Breeding territories.*—Most territories were established in 1976–77 aspen habitat, whereas few territories were located in 1980–81 aspen habitat (Table 5). Seventy percent of the total territories were those of ground-shrub foragers, which were located mainly in 1976–77 aspen and 1976–77 oak habitats. The remaining territories were established by trunk-bark and sallier-canopy foraging species, and these were positioned primarily in uncut habitats at the BGMA.

*Relationships among habitat types.*—Based on avian population and community variables, the six habitat types at the BGMA comprised two groups, corresponding to two factors extracted by factor analysis. Factor I associated the uncut habitats (factor loadings $\geq 0.86$) and explained 81% of the variance. This factor, which is labeled a "breeding-season ground-shrub forager" factor, grouped habitat types characterized by unstable populations (high CV of mean density) of ground-shrub foraging species during the breeding season. For example, the CV of mean density for the Field Sparrow ranged from 227–381% in uncut habitats compared to only 61–141% in clearcut habitats.

Factor II, in contrast, grouped the three clearcut habitats and accounted for 15% of the variation. Factor II is termed a "winter-season trunk-bark forager" factor because the CV of both mean *S* and total density for the trunk-bark foraging guild and the CV of mean total density for the Black-capped Chickadees during winter in uncut habitats were much lower than those in clearcut habitats. For instance, the CV of mean total density for trunk-bark foragers varied from 195–548% in clearcut habitats versus only 92–141% in uncut habitats.

*Winter avian-habitat relationships.*—Avian variables, such as mean *S*, *H'*, and total density for all species combined and for the trunk-bark foraging guild were positively correlated with habitat variables describing the vegetative structure of a relatively mature forest stand, including high overstory tree density, high growth-form diversity, and low understory tree and shrub densities (Table 6). Mean density of the three common species also was directly associated with these habitat variables. In contrast, mean *S*, *H'*, and total density for the ground-shrub forager guild were directly correlated with high densities of understory trees, tall shrubs, and short shrubs, which represent vegetative structure typical of clearcut habitats.

TABLE 3

CUMULATIVE NUMBER OF SPECIES, MEANS (± SD) OF BREEDING AVIAN COMMUNITY VARIABLES, AND IMPORTANCE VALUES OF THREE GUILDS IN SIX HABITATS AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE SEASONS (1982–1984)

| Variable | Habitat type | | | | | |
|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak |
| Cumulative no. species: | | | | | | |
| All species combined | 43 | 47 | 35[a] | 16 | 51[b] | 30 |
| Ground-shrub forager | 22 | 23 | 21 | 14 | 19 | 17 |
| Trunk-bark forager | 5 | 8 | 3 | 1 | 9 | 5 |
| Sallier-canopy forager | 16 | 16 | 10 | 1 | 21 | 8 |
| Species richness (*S*): | | | | | | |
| All species combined[c] | 6.2 ± 3.6†* | 8.8 ± 3.7+ | 8.0 ± 2.8†+ | 3.1 ± 1.9 | 6.8 ± 3.9†* | 5.2 ± 2.1* |
| Ground-shrub forager[c] | 3.7 ± 2.4†* | 4.6 ± 2.1† | 6.0 ± 2.1 | 3.0 ± 1.7* | 3.2 ± 2.0* | 4.2 ± 1.8†* |
| Trunk-bark forager[c] | 1.3 ± 1.2†* | 2.0 ± 1.1† | 1.0 ± 0.8* | 0.1 ± 0.3+ | 1.3 ± 1.2†* | 0.3 ± 0.6+ |
| Sallier-canopy forager[d] | 1.5 ± 1.6†* | 2.2 ± 1.5† | 1.0 ± 0.9* | 0.1 ± 0.3+ | 2.8 ± 1.7† | 0.7 ± 0.8*+ |
| Species diversity (*H'*): | | | | | | |
| All species combined[c] | 1.6 ± 0.5†* | 1.9 ± 0.6+ | 1.8 ± 0.5†+ | 0.9 ± 0.6 | 1.7 ± 0.6†*+ | 1.4 ± 0.5* |
| Ground-shrub forager | 1.0 ± 0.7 | 1.3 ± 0.6 | 1.6 ± 0.5 | 0.9 ± 0.5 | 0.9 ± 0.5 | 1.2 ± 0.5 |
| Trunk-bark forager[d] | 0.3 ± 0.5†* | 0.5 ± 0.5† | 0.2 ± 0.3* | 0.0 ± 0.0+ | 0.3 ± 0.5† | 0.0 ± 0.2*+ |
| Sallier-canopy forager[d] | 0.4 ± 0.6†* | 0.7 ± 0.6† | 0.2 ± 0.3*+ | 0.0 ± 0.0+ | 0.8 ± 0.7† | 0.1 ± 0.3*+ |

TABLE 3
CONTINUED

| Variable | Habitat type | | | | | |
|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak |
| Total density (no./10 ha): | | | | | | |
| All species combined[c] | 28.1 ± 19.8 | 42.3 ± 18.3 | 54.4 ± 20.6 | 21.5 ± 15.8 | 35.0 ± 21.0 | 39.6 ± 17.4 |
| Ground-shrub forager[c] | 15.2 ± 11.3† | 23.8 ± 12.7† | 45.0 ± 18.0 | 21.1 ± 15.5† | 15.7 ± 9.4† | 34.9 ± 16.8 |
| Trunk-bark forager[d] | 5.4 ± 4.8†* | 10.0 ± 5.5 | 5.7 ± 5.3* | 1.2 ± 5.5+ | 7.4 ± 8.0†* | 1.8 ± 4.4+ |
| Sallier-canopy forager[d] | 7.6 ± 8.4† | 8.6 ± 5.7† | 3.9 ± 3.7* | 1.2 ± 5.5+ | 12.3 ± 12.8† | 3.0 ± 3.9* |
| Importance value (*IV*)[e]: | | | | | | |
| Ground-shrub forager | 131 | 146 | 200 | 140 | 128 | 173 |
| Trunk-bark forager | 85 | 119 | 86 | 12 | 84 | 24 |
| Sallier-canopy forager | 84 | 102 | 72 | 12 | 117 | 54 |

[a] Includes one sighting of a Great Horned Owl (*Bubo virginianus*).
[b] Includes one sighting each of a Red-tailed Hawk and a Great Horned Owl.
[c] Significant difference among habitat types; $F \geq 4.42$, df = 5,142, $P < 0.05$; single-classification ANOVA. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; Student-Newman-Keuls test.
[d] Significant difference among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.
[e] An *IV* based on the sum of the proportion of total censuses (×100) in which a guild was present in a given habitat type (maximum = 30 censuses for ground-shrub forager in 1976–77 aspen) and the relative density of a guild in a given habitat type (maximum = 44.96/10 ha for ground-shrub forager in 1976–77 aspen); maximum value of *IV* = 200.

TABLE 4

MEAN (± SD), DENSITY (NO./10 HA), AND IMPORTANCE VALUE FOR 16 COMMON SPECIES IN SIX HABITAT TYPES AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA DURING THREE BREEDING SEASONS (1982–1984)

| Species | Habitat type | | | | | |
|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak |
| Downy Woodpecker[a] (*Picoides pubescens*) | 0.8 ± 1.7†* (30)[b] | 1.2 ± 2.4† (42) | 0.0 ± 0.0* (0) | 0.2 ± 0.8†* (9) | 1.0 ± 2.8†* (25) | 0.1 ± 0.6†* (5) |
| Blue Jay (*Cyanocitta cristata*) | 0.9 ± 1.7†* (36) | 2.6 ± 4.3† (74) | 0.2 ± 0.8* (9) | 0.0 ± 0.0 (0) | 4.8 ± 6.6† (111) | 0.2 ± 0.8* (9) |
| Black-capped Chickadee (*Parus atricapillus*) | 2.6 ± 3.6†*+ (74) | 4.2 ± 3.8†* (124) | 4.4 ± 4.6† (123) | 0.0 ± 0.0§ (0) | 1.9 ± 3.6*+ (47) | 1.1 ± 3.9+§ (22) |
| Gray Catbird (*Dumetella carolinensis*) | 0.0 ± 0.0† (0) | 0.9 ± 1.7†* (35) | 4.7 ± 4.3*+ (121) | 1.1 ± 2.0†* (41) | 0.4 ± 1.2† (25) | 7.3 ± 5.6 (163) |
| Red-eyed Vireo (*Vireo olivaceus*) | 1.9 ± 3.0† (60) | 1.2 ± 1.9† (49) | 0.0 ± 0.0* (0) | 0.0 ± 0.0* (0) | 1.0 ± 1.8† (44) | 0.4 ± 1.2†* (19) |
| Black-and-white Warbler (*Mniotilta varia*) | 0.4 ± 1.5†*+ (16) | 3.1 ± 3.0§ (99) | 1.1 ± 1.8†+ (44) | 0.0 ± 0.0* (0) | 2.2 ± 2.9+§ (76) | 0.2 ± 0.8†* (9) |
| Golden-winged Warbler (*Vermivora chrysoptera*) | 0.3 ± 1.0† (14) | 0.9 ± 2.1†* (28) | 4.6 ± 4.0+ (116) | 0.6 ± 1.5†* (21) | 0.1 ± 0.6† (5) | 2.0 ± 2.3*+ (76) |
| Nashville Warbler (*Vermivora ruficapilla*) | 1.2 ± 2.2† (42) | 1.0 ± 1.8† (48*) | 0.9 ± 1.7†* (35) | 0.0 ± 0.0* (0) | 0.7 ± 1.6†* (21) | 0.3 ± 1.8†* (27) |
| Chestnut-sided Warbler (*Dendroica pensylvanica*) | 0.4 ± 3.5† (16) | 0.9 ± 1.7†* (35) | 4.0 ± 3.8+ (110) | 0.2 ± 0.8† (9) | 0.3 ± 1.0† (9) | 2.4 ± 3.0*+ (77) |

TABLE 4
CONTINUED

| Species | Habitat type | | | | | |
|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak |
| Ovenbird (*Seiurus aurocapillus*) | 3.0 ± 2.5† (104) | 3.2 ± 2.8† (103) | 0.2 ± 0.8* (9) | 0.0 ± 0.0* (0) | .9 ± 3.2† (120) | 0.1 ± 0.6* (5) |
| Common Yellowthroat (*Geothlypis trichas*) | 0.4 ± 1.2† (19) | 0.9 ± 1.7† (35) | 7.5 ± 6.3*+ (161) | 3.6 ± 3.9* (106) | 0.6 ± 1.3† (25) | 8.4 ± 7.0+ (170) |
| Brown-headed Cowbird (*Molothrus ater*) | 2.8 ± 3.8† (80) | 2.0 ± 2.6† (72) | 1.2 ± 2.4†* (42) | 0.0 ± 0.0+ (0) | 0.8 ± 1.7†*+ (30) | 0.1 ± 0.6*+ (5) |
| Indigo Bunting (*Passerina cyanea*) | 0.6 ± 1.3† (25) | 1.1 ± 1.6† (48) | 2.0 ± 2.4* (72) | 0.8 ± 1.7† (30) | 0.2 ± 0.8† (9) | 1.6 ± 2.6 (49) |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 2.1 ± 2.4†* (77) | 6.3 ± 5.3+ (153) | 9.9 ± 6.8+ (185) | 6.1 ± 5.7†+ (143) | 1.7 ± 2.3* (56) | 9.9 ± 5.5+ (200) |
| Chipping Sparrow (*Spizella passerina*) | 0.2 ± 0.8†* (9) | 2.0 ± 2.9+ (64) | 1.0 ± 1.8†+ (40) | 0.2 ± 0.8†* (9) | 0.0 ± 0.0* (0) | 0.0 ± 0.0* (0) |
| Field Sparrow (*Spizella pusilla*) | 0.7 ± 1.8†* (22) | 0.6 ± 1.3†* (25) | 7.4 ± 4.5+ (171) | 8.1 ± 7.3+ (167) | 0.3 ± 1.0† (9) | 3.0 ± 4.2*+ (78) |

[a] Density of each species was significantly different among habitat types; $\chi^2 \geq 11.07$, df = 5, $P < 0.05$; Kruskal-Wallis test. Nonsignificant differences ($P > 0.05$) between habitat types are indicated by similar symbols; STP test.

[b] Importance values (*IV*) are based on the sum of the relative number of total censuses in which a species was present in a given habitat type (maximum = 27 censuses for Rufous-sided Towhee in 1976–77 oak) and the relative density of a species in a given habitat type (maximum = 9.88/10 ha for Rufous-sided Towhee in 1976–77 aspen and 1976–77 oak); maximum value of $IV = 200$.

TABLE 5

CUMULATIVE NUMBER OF TERRITORIES PER INDIVIDUAL SPECIES WITH >10 TERRITORIES, CUMULATIVE NUMBER OF TERRITORIES FOR ALL SPECIES COMBINED, CUMULATIVE PROPORTION (%) OF TOTAL TERRITORIES PER FORAGING GUILD, AND TOTAL NUMBER OF SPECIES ESTABLISHING BREEDING TERRITORIES (1982–1984)

| | Habitat type | | | | | | |
|---|---|---|---|---|---|---|---|
| | Control | Mature aspen | 1976–77 aspen | 1980–81 aspen | Mature oak | 1976–77 oak | Total |
| No. territories per species: | | | | | | | |
| Gray Catbird | 0.0 | 0.6 | 6.2 | 0.2 | 0.0 | 8.5 | 15.5 |
| Black-and-white Warbler | 0.5 | 5.0 | 1.5 | 0.2 | 3.0 | 0.4 | 10.6 |
| Golden-winged Warbler | 0.0 | 0.4 | 7.5 | 0.9 | 0.0 | 3.0 | 11.8 |
| Chestnut-sided Warbler | 0.2 | 0.2 | 6.0 | 0.4 | 0.2 | 4.0 | 11.0 |
| Ovenbird | 3.5 | 5.0 | 0.0 | 0.0 | 5.7 | 0.0 | 14.2 |
| Common Yellowthroat | 0.7 | 0.6 | 10.4 | 5.2 | 0.0 | 9.5 | 26.4 |
| Indigo Bunting | 0.5 | 0.9 | 4.6 | 1.4 | 0.2 | 2.5 | 10.1 |
| Rufous-sided Towhee | 1.6 | 5.1 | 8.5 | 4.6 | 2.2 | 7.5 | 29.5 |
| Field Sparrow | 0.5 | 0.0 | 7.7 | 5.0 | 0.2 | 2.5 | 15.9 |
| Total no. territories, all species | 24.4 | 38.1 | 61.3 | 18.5 | 29.3 | 39.7 | 211.3 |
| % total no. territories, ground-shrub foragers | 50 | 52 | 84 | 90 | 44 | 89 | 70 |
| % total no. territories, trunk-bark foragers | 16 | 22 | 6 | 2 | 17 | 9 | 12 |
| % total no. territories, sallier-canopy foragers | 34 | 26 | 10 | 8 | 39 | 2 | 18 |
| No. species establishing territories | 21 | 22 | 16 | 11 | 19 | 16 | 32 |

Several avian variables, including mean *S*, *H'*, and total density for the trunk-bark foraging guild and mean density for Downy Woodpeckers and Black-capped Chickadees, were directly associated with density and basal area of overstory *Populus*, *Quercus*, and snags. In contrast, mean *S*, *H'*, and total density for the ground-shrub foraging guild were positively correlated with short shrub densities of *Q. ilicifolia* and *Q. prinoides* combined and *P. serotina*.

*Breeding avian-habitat relationships.*—Several variables describing the total avian community, the trunk-bark foraging guild, and the sallier-canopy foraging guild were positively related to habitat variables, such as overstory tree density, canopy coverage, and growth-form diversity (Table 7). As in winter, the ground-shrub foraging guild was directly correlated with understory tree and tall shrub densities.

TABLE 6

CORRELATIONS BETWEEN VARIABLES DESCRIBING VEGETATIVE STRUCTURE AND THE AVIAN COMMUNITY OR POPULATIONS IN SIX HABITATS DURING THREE WINTERS (1982–1984)

| Avian variable[a] | Vegetation variable | | | | | |
|---|---|---|---|---|---|---|
| | Density overstory trees | Basal area overstory trees | Density understory trees | Density tall shrubs | Density short shrubs | Growth-form diversity |
| Species richness ($S$): | | | | | | |
| All species, $\bar{x}$ | 0.95* | 0.90* | | | −0.92† | 0.94* |
| All species, CV | −0.87* | | −0.91† | | | −0.95* |
| Trunk-bark foragers, $\bar{x}$ | 0.95* | 0.91* | | | −0.91* | 0.90* |
| Trunk-bark foragers, CV | −0.92* | −0.82* | −0.83* | | | −0.95* |
| Species diversity ($H'$): | | | | | | |
| All species, $\bar{x}$ | 0.89* | 0.90* | | | −0.93* | 0.83* |
| All species, CV | −0.91* | | | | 0.92† | |
| Trunk-bark foragers, $\bar{x}$ | 0.85* | 0.86* | | | −0.95* | 0.82* |
| Trunk-bark foragers, CV | −0.94† | −0.92† | | 0.91† | 0.94† | |
| Total density: | | | | | | |
| All species, $\bar{x}$ | 0.97* | 0.93† | | | −0.91† | 0.94* |
| All species, CV | −0.87* | | −0.93† | | | −0.94* |
| Trunk-bark foragers, $\bar{x}$ | 0.97* | 0.94† | | | 0.94† | 0.95* |
| Trunk-bark foragers, CV | −0.89* | | −0.87* | | | −0.96* |
| Species density: | | | | | | |
| Downy Woodpecker, $\bar{x}$ | 0.95† | 0.97† | | | −0.92† | 0.84* |
| Downy Woodpecker, CV | −0.93† | −0.93† | | 0.88† | 0.88* | −0.98† |
| Black-capped Chickadee, $\bar{x}$ | 0.95* | 0.88* | | | | 0.96* |
| Black-capped Chickadee, CV | −0.83* | | −0.88† | | | −0.93* |
| White-breasted Nuthatch, $\bar{x}$ | | 0.82* | | | 0.92* | |
| White-breasted Nuthatch, CV | −0.96† | −0.95† | | 0.92† | 0.97* | −0.92† |

[a] Only significant correlations ($P < 0.05$) are included; a significant $r$ is based on untransformed (†) or log-transformed (*) data; no sign designates a positive correlation, and a negative sign indicates a negative correlation.

TABLE 7

CORRELATIONS BETWEEN VARIABLES DESCRIBING VEGETATIVE STRUCTURE AND THE AVIAN COMMUNITY IN SIX HABITATS DURING THREE BREEDING SEASONS (1982–1984)

| | Vegetation variable | | | | | | |
|---|---|---|---|---|---|---|---|
| Avian variable[a] | Density overstory trees | Basal area overstory trees | Density understory trees | Density tall shrubs | Density short shrubs | Percent canopy coverage | Growth-form diversity |
| Cumulative no. species: | | | | | | | |
| All species | 0.91* | 0.82* | 0.84* | | | 0.96* | 0.97* |
| Trunk-bark foragers | 0.91* | 0.91* | | | −0.91* | 0.94† | |
| Sallier-canopy foragers | 0.92* | 0.85† | 0.82* | | −0.82* | 0.98* | 0.87* |
| Cumulative no. territories: | | | | | | | |
| All species | | | 0.91† | 0.91* | | | |
| Ground-shrub foragers | | | 0.86† | | | | |
| Trunk-bark foragers | | | | | | | 0.90* |
| Sallier-canopy foragers | 0.90† | 0.91† | | | | 0.90* | 0.96* |
| Species richness ($S$): | | | | | | | |
| All species, $\bar{x}$ | | | 0.87* | | | | 0.86* |
| All species, CV | | | | −0.89* | | | |
| Ground-shrub foragers, $\bar{x}$ | | | | 0.89† | | | |
| Trunk-bark foragers, $\bar{x}$ | | | | | | | 0.93* |
| Trunk-bark foragers, CV | | | | −0.85† | | | −0.94† |
| Sallier-canopy foragers, $\bar{x}$ | 0.90† | 0.91† | | | | 0.89* | 0.92* |
| Sallier-canopy foragers, CV | | | 0.94* | | | −0.87* | −0.91* |

TABLE 7
CONTINUED

| Avian variable[a] | Vegetation variable | | | | | | |
|---|---|---|---|---|---|---|---|
| | Density overstory trees | Basal area overstory trees | Density understory trees | Density tall shrubs | Density short shrubs | Percent canopy coverage | Growth-form diversity |
| Species diversity ($H'$): | | | | | | | |
| All species, $\bar{x}$ | | | 0.89* | | | | 0.84† |
| All species, CV | | | −0.95† | | | | −0.82† |
| Ground-shrub foragers, $\bar{x}$ | | | | 0.88† | | | |
| Trunk-bark foragers, $\bar{x}$ | 0.83† | 0.84* | | | | | 0.87* |
| Sallier-canopy foragers, $\bar{x}$ | 0.92† | 0.92† | | | | 0.82* | 0.86* |
| Total density: | | | | | | | |
| All species, $\bar{x}$ | | | 0.82† | 0.88* | | | |
| All species, CV | | | | −0.87† | | | |
| Ground-shrub foragers, $\bar{x}$ | | | | 0.86† | 0.84* | | |
| Ground-shrub foragers, CV | | | | −0.87† | | | |
| Trunk-bark foragers, $\bar{x}$ | | | 0.82* | | | 0.83* | 0.95* |
| Trunk-bark foragers, CV | | | −0.82* | | | | −0.95† |
| Sallier-canopy foragers, $\bar{x}$ | 0.93† | 0.94† | 0.83* | | | 0.95* | 0.96* |
| Sallier-canopy foragers, CV | | | −0.92* | | | −0.84* | −0.88* |

[a] Only significant correlations ($P < 0.05$) are included; a significant $r$ is based on untransformed (†) or log-transformed (*) data; no sign designates a positive correlation, and a negative sign indicates a negative correlation.

Density and basal area of overstory *Populus, Quercus,* and snags were directly correlated with mean *S, H'*, and total density for all species combined, as well as with the trunk-bark and sallier-canopy foraging guilds. Negative relationships were found between these avian variables and short shrub densities of *Q. ilicifolia* and *Q. prinoides* combined and *P. serotina.* In contrast, mean *S, H'*, and total density for ground-shrub foragers were positively associated with tall shrub densities of *Populus, Q. ilicifolia* and *Q. prinoides* combined, and *P. serotina.*

Mean density and cumulative number of territories of Downy Woodpeckers, Blue Jays, Red-eyed Vireos, Ovenbirds, and Brown-headed Cowbirds were positively correlated with several variables describing the structure of overstory trees (Table 8), and to density and basal area of individual overstory species (e.g., *Populus, Quercus, Carya, Pinus*), and snags. In comparison, mean density and cumulative number of territories of Common Yellowthroats, Rufous-sided Towhees, and Field Sparrows were inversely associated with these overstory structural and composition variables. Mean density and cumulative number of territories of a few species (e.g., Black-capped Chickadees) were positively related to total understory tree, tall shrub, or short shrub densities, and to densities of individual species (e.g., *Populus, Q. ilicifolia* and *Q. prinoides* combined, and *P. serotina*).

## DISCUSSION

As in other northern latitudes, avifauna in all six habitat types at the BGMA was depauperate in winter compared to that during the breeding season (see Rotenberry et al. 1979). In contrast, avian density and diversity in southern latitudes of the United States peak during winter because of the presence of both permanent residents and a large number of wintering species that later migrate northward to breed (Dickson 1978). Moreover, habitats in southern regions have a milder climate and a greater abundance of food resources in winter relative to those in northern regions (Dickson 1978).

Greater density, diversity, and temporal stability of the wintering avian community, particularly the trunk-bark foraging guild, in uncut habitats at the BGMA suggest that resources (e.g., food and cover) were more abundant and predictable there than in early-successional, clearcut habitats (after Kricher 1975, Conner et al. 1979). Uncut habitats at the BGMA, characterized by abundant overstory trees and snags, provided cover and foraging substrata for wintering woodpeckers, nuthatches, and parids (see Conner et al. 1979, Briggs et al. 1982). Further, many overstory trees in uncut habitats are rough-barked *Quercus* and *Pinus,* which provide mast and seed as food as well as increasing the surface area upon which birds

can forage for crevice-dwelling arthropods (Brawn et al. 1982). Black-capped Chickadees were best adapted to the wide range of habitat types at the BGMA during winter. Chickadees typically are abundant and widely distributed components of a wintering bird community (e.g., Back 1979, Conner et al. 1979) and are characteristic of both forest edges and interiors (Brewer 1963).

A lack of wintering ground-shrub foragers at the BGMA was partly due to a scarcity of weed seeds and the presence of snow or ice cover. Seed-producing forbs and grasses were primarily restricted to areas along the unimproved dirt road; snow and ice cover was present each winter during the study, which conceivably could increase energetic costs associated with foraging in either leaf litter or vegetation near ground level. Similarly, abundance and distribution of granivorous species or those that forage near ground level may be restricted in Midwest farmlands during winter due to these factors (Vance 1976; Yahner 1981, 1983b). Conversely, in even-aged stands of southern latitudes with limited or no snow cover, birds that forage at or near ground level are often the most abundant species in the wintering avian community (Hagar 1960, Blake 1982).

In contrast to avian community structure in winter, community structure in summer was not always more complex in older habitats at the BGMA. For example, species richness did not vary between 1976–77 aspen and uncut aspen habitats. Similarities in avian community structure among habitat types of different age were partially attributed to individual territories overlapping more than one stand. For instance, Black-capped Chickadees foraged primarily within portions of territories located in uncut aspen stands, but also foraged to a limited extent in contiguous 1976–77 aspen stands. Conversely, some species, such as Chestnut-sided Warblers, located most territories in clearcut habitats, yet used overstory trees as song perches along edges of proximal uncut habitats (see Strelke and Dickson 1980).

Species foraging at or near ground level during the breeding season are typically well represented in clearcut or selectively harvested forests (Franzreb and Ohmart 1978, Conner et al. 1979). In my study, high shrub density, which provided readily available foraging and nesting microhabitats for species such as Chestnut-sided Warblers and Rufous-sided Towhees partially accounted for high density, diversity, and temporal stability of the ground-shrub foraging guild in 1976–77 clearcut habitats. On the other hand, the trunk-bark and canopy-sallier foraging guilds were abundant and relatively stable in uncut compared to clearcut habitats at the BGMA, perhaps because uncut habitats contained overstory trees and snags as foraging and nesting sites (Crawford et al. 1981, Maurer et al. 1981).

TABLE 8

CORRELATIONS BETWEEN VARIABLES DESCRIBING VEGETATIVE STRUCTURE AND AVIAN POPULATIONS IN SIX HABITAT TYPES DURING THREE BREEDING SEASONS (1982–1984)

| | Vegetation variable | | | | | | |
|---|---|---|---|---|---|---|---|
| Avian variable[a] | Density overstory trees | Basal area overstory trees | Density understory trees | Density tall shrubs | Density short shrubs | Percent canopy coverage | Growth-form diversity |
| Downy Woodpecker, $\bar{x}$ | 0.94† | 0.95* | | | | 0.83† | |
| Downy Woodpecker, $T$[b] | 0.99† | 0.99† | | | −0.85* | 0.95† | 0.84† |
| Blue Jay, $\bar{x}$ | 0.88* | 0.89* | | | | | |
| Blue Jay, $T$ | 0.95† | 0.97* | | | | 0.84† | 0.82* |
| Black-capped Chickadee, $\bar{x}$ | | | 0.86† | | | | 0.82* |
| Gray Catbird, $T$ | | | | 0.85† | | | |
| Red-eyed Vireo, $\bar{x}$ | 0.96* | 0.92* | | | −0.95† | 0.97† | 0.87* |
| Red-eyed Vireo, CV | −0.89* | −0.91* | | | | | |
| Red-eyed Vireo, $T$ | 0.98† | 0.97* | | | −0.90* | 0.99† | 0.82* |
| Black-and-white Warbler, CV | | | 0.94* | 0.85* | | | |
| Golden-winged Warbler, $\bar{x}$ | | | | 0.85† | | | |
| Golden-winged Warbler, $T$ | | −0.82* | | | 0.82* | | |
| Nashville Warbler, $\bar{x}$ | | | | | | | 0.92* |
| Nashville Warbler, $T$ | | | | | | | 0.87* |
| Chestnut-sided Warbler, $\bar{x}$ | | | | 0.93† | | | |
| Chestnut-sided Warbler, CV | | | | −0.95† | | | |
| Chestnut-sided Warbler, $T$ | | | | 0.88† | | | |

TABLE 8
CONTINUED

| Avian variable[a] | Vegetation variable | | | | | | |
|---|---|---|---|---|---|---|---|
| | Density overstory trees | Basal area overstory trees | Density understory trees | Density tall shrubs | Density short shrubs | Percent canopy coverage | Growth-form diversity |
| Ovenbird, $\bar{x}$ | 0.99† | 0.99† | | | −0.83* | 0.93† | 0.85* |
| Ovenbird, $T$ | 0.98† | 0.99* | | | | 0.87† | |
| Common Yellowthroat, $\bar{x}$ | −0.88† | −0.95† | | | 0.86* | | |
| Common Yellowthroat, CV | | | −0.90† | −0.95* | | | |
| Common Yellowthroat, $T$ | −0.92† | −0.97* | | | 0.85† | −0.82† | |
| Brown-headed Cowbird, $\bar{x}$ | 0.83† | 0.86* | | | | 0.88* | |
| Brown-headed Cowbird, $T$ | 0.90† | | | | −0.89† | 0.88† | 0.87* |
| Indigo Bunting, CV | | | | 0.85† | | | |
| Indigo Bunting, $T$ | | −0.86* | | | 0.84* | | |
| Rufous-sided Towhee, $\bar{x}$ | −0.83† | −0.85† | | | 0.88† | | |
| Rufous-sided Towhee, $T$ | | | | | 0.94* | | |
| Field Sparrow, $\bar{x}$ | −0.99* | −0.95* | | | 0.82* | −0.93† | |
| Field Sparrow, CV | 0.93† | 0.95† | | | 0.86* | 0.90† | |
| Field Sparrow, $T$ | −0.95* | −0.94* | | | | −0.89* | |

[a] Only significant correlations ($P < 0.05$) are included; a significant $r$ is based on untransformed (†) or log-transformed (*) data; no sign designates a positive correlation, and a negative sign indicates a negative correlation.
[b] $T$ = cumulative number of territories.

Rufous-sided Towhees presumably were best adapted to the various habitat types at the BGMA during the breeding season. This species is associated with forest edges or forests with dense understory (Forman et al. 1976, Casey and Hein 1983). At the BGMA, density of towhees was related to high density of certain shrub species (e.g., *Q. ilicifolia*) that were characteristic of both clearcut habitats and mature aspen habitat (Yahner and Grimm 1984). Several other common ground-shrub foragers, including Gray Catbirds, Golden-winged Warblers, Chestnut-sided Warblers, and Field Sparrows, probably also were benefited by the grouse habitat management study. These species typically occur in clearcut stands, forest openings, or forest edges with dense shrub or understory growth (Forman et al. 1976, Butcher et al. 1981, Crawford et al. 1981, Casey and Hein 1983). Red-eyed Vireos and Ovenbirds, however, which are examples of forest-interior species (Galli et al. 1976, Forman et al. 1976), apparently were unaffected by habitat fragmentation resulting from the current cutting cycle (see also Yahner 1984). Of the 16 common breeding species at the BGMA, eight species (Blue Jays, Black-capped Chickadees, Gray Catbirds, Red-eyed Vireos, Black-and-white Warblers, Chestnut-sided Warblers, Common Yellowthroats, Indigo Buntings) have showed significant population increases in Pennsylvania or in the eastern United States over the past couple of decades (Anderson et al. 1981). Conversely, two of the 16 species (Golden-winged Warblers and Rufous-sided Towhees) have shown recent statewide or regional declines (Anderson et al. 1981).

Conner et al. (1979) concluded that, in Virginia, large clearcut stands (20–30 ha) generally had a negative impact on avifauna, but that the effects of forest clearcutting on avian communities varied with season, seral stage, and bird species. At the BGMA, the mosaic of small, one-ha stands has increased vegetative diversity within a localized area, thereby attracting a variety of avian species adapted to different foraging and nesting microhabitats. No evidence is available to suggest that the grouse habitat management study has negatively impacted the distribution and abundance of wintering or breeding avifauna, although the effects of this plan on productivity due to nest predation or parasitism (see Whitcomb et al. 1981) have not been addressed. Yahner and Wright (1985), however, recently found that predation on artificial ground nests on the treated sector was less in both 1976–77 aspen and 1980–81 aspen habitats than in mature aspen habitat.

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# LATE SUMMER–SPRING MOVEMENTS OF JUVENILE SAGE GROUSE

PETER O. DUNN[1] AND CLAIT E. BRAUN[2]

ABSTRACT.—Late summer to early spring movements of radio-marked juvenile Sage Grouse (*Centrocercus urophasianus*) were studied on Cold Spring Mountain, northwestern Colorado, from July to February 1981–82 and August to May 1982–83. Movements were analyzed from 118 locations (N = 8 grouse) during July–November 1981 and 213 locations (N = 10 grouse) during August–November 1982. Grouse steadily moved away from capture sites until November each year when they moved to winter-use sites. Movements to wintering areas in late November were related to snowfall and subsequent availability of sagebrush. Maximum one-way distance to wintering areas was 30.3 km (N = 4 radio-marked grouse). Sage Grouse generally followed topographic features and avoided areas without sagebrush cover, although they were capable of long-distance (23 km) movements over areas without shrub cover. During spring recruitment there appeared to be roving groups of males, probably yearlings, that spent much of the breeding season displaying near females away from traditional leks. *Received 25 Feb. 1985, accepted 10 July 1985.*

Spacing behavior may produce changes in birth, death, and movement rates that subsequently limit population size (reviewed in Watson and Moss 1970, Krebs 1978). Red Grouse (*Lagopus lagopus scoticus*) are a classic example of the importance of summer and fall movements to recruitment into the breeding population (Moss et al. 1984). Although natal movements have been examined for Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) (Bowman and Robel 1977), Spruce Grouse (*Dendragapus canadensis*) (Keppie 1979), and Blue Grouse (*D. obscurus*) (Jamieson and Zwickel 1983a), movements of juvenile Sage Grouse (*Centrocercus urophasianus*) from summer ranges to breeding areas have not been studied. In this paper we present the first detailed report of the late-summer to early-spring movements of juvenile Sage Grouse.

## STUDY AREA AND METHODS

The study was conducted on Cold Spring Mountain in northwestern Moffat County, Colorado, and in adjacent Wyoming and Utah from July 1981 through June 1983. The study area is semiarid sagebrush (*Artemisia* spp.) rangeland with interspersed quaking aspen (*Populus tremuloides*) and pinyon pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) stands, and meadows. Lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) occur above 2620 m on Middle Mountain (2904 m) and Diamond Peak (2909 m) on the northern edge of the study area. Cold Spring Mountain (2622 m) receives 46–51 cm

[1] Dept. Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, Colorado 80523; (Present address: Dept. Zoology, Univ. Alberta. Edmonton, Alberta T6G 2E9, Canada.)
[2] Colorado Division of Wildlife Research Center, 317 W. Prospect Rd., Fort Collins, Colorado 80526.

of precipitation annually, of which 11% falls in August (U.S. Dept. Interior 1978). July-August trapping on Cold Spring Mountain yielded 120 to >300 banded juvenile Sage Grouse per year from 1978 through 1982.

Juvenile grouse were captured and individually marked with numbered aluminum bands and unique combinations of colored plastic bands in 1981 and 1982. Drive traps, a bumper-mounted cannon net, and spotlights and long-handled nets were used to capture grouse (Giesen et al. 1982). Captured birds were classified to sex and age by wing molt and length of primaries (Beck et al. 1975). Forty-two radio transmitters attached to poncho-type markers (Amstrup 1980) were placed on juvenile grouse during July and August 1981 and July through October 1982. Thirteen solar-powered radio transmitters were used in 1981, and 23 battery-powered and 6 solar-powered radio transmitters were used in 1982. Radio-marked birds were relocated at least three times weekly from 15 July to 31 August 1981 and from 1 August to 11 September 1982. Relocations were made at least monthly after 11 September to 15 November each year. During January to mid-April 1983, 4 radio-marked juveniles were relocated at least once a month. Weekly radio relocations were evenly divided into morning (≤4 h after sunrise), midday (>4 h after sunrise to >4 h before sunset), and evening (≤4 h before sunset) time periods. These time periods coincide with most feeding during morning and evenings, and roosting during midday. Radiolocations made on the ground were determined by triangulation at close range (approximately 200 m) or by flushing, and data were plotted on 7.5-min U.S. Geological Survey topographic maps. This was supplemented with radio-tracking from an aircraft on 3 November 1981 and 15 January 1983.

Distances moved by grouse from their capture sites were analyzed with 2-way analysis of variance (ANOVA) for interactions among individual birds and time periods. If the interaction was significant ($P < 0.05$), distance from capture site for each bird was regressed individually on other variables (age of bird, date, or movement rate). Directions were analyzed with nonparametric statistical tests (Batschelet 1978). Test results were considered significant at the 0.05 probability level.

## RESULTS

Fifteen and 43 juvenile Sage Grouse were radiomarked in 1981 and 1982, respectively. Locations of only 8 birds in 1981 and 10 birds in 1982 were used for analysis because of radio signal losses, predation, hunter harvest, or incomplete data. Movements were analyzed from 118 locations in 1981 and 213 locations in 1982.

During both years grouse steadily moved away from their capture sites from August to November (Fig. 1). Because of unequal sample sizes and interaction effects (2-way ANOVA, $P = 0.01$) between individual birds and time periods, it was not possible to determine when increases in distances from capture sites occurred; however, the data indicate that increases were gradual during both years. Movement rates (km/day) did not vary with date in either year (Table 1). Distance from capture sites was highly correlated with date for 14 of 18 birds (Table 1). Three birds showed no relationship between distance from capture sites and date, age of bird, or movement rate. During 15 July to 4 September 1981 and 1 August to 4 September 1982, 84 and 78% of all locations (79/94 and 72/92, respectively) were ≤2 km from capture sites, while during 3 October

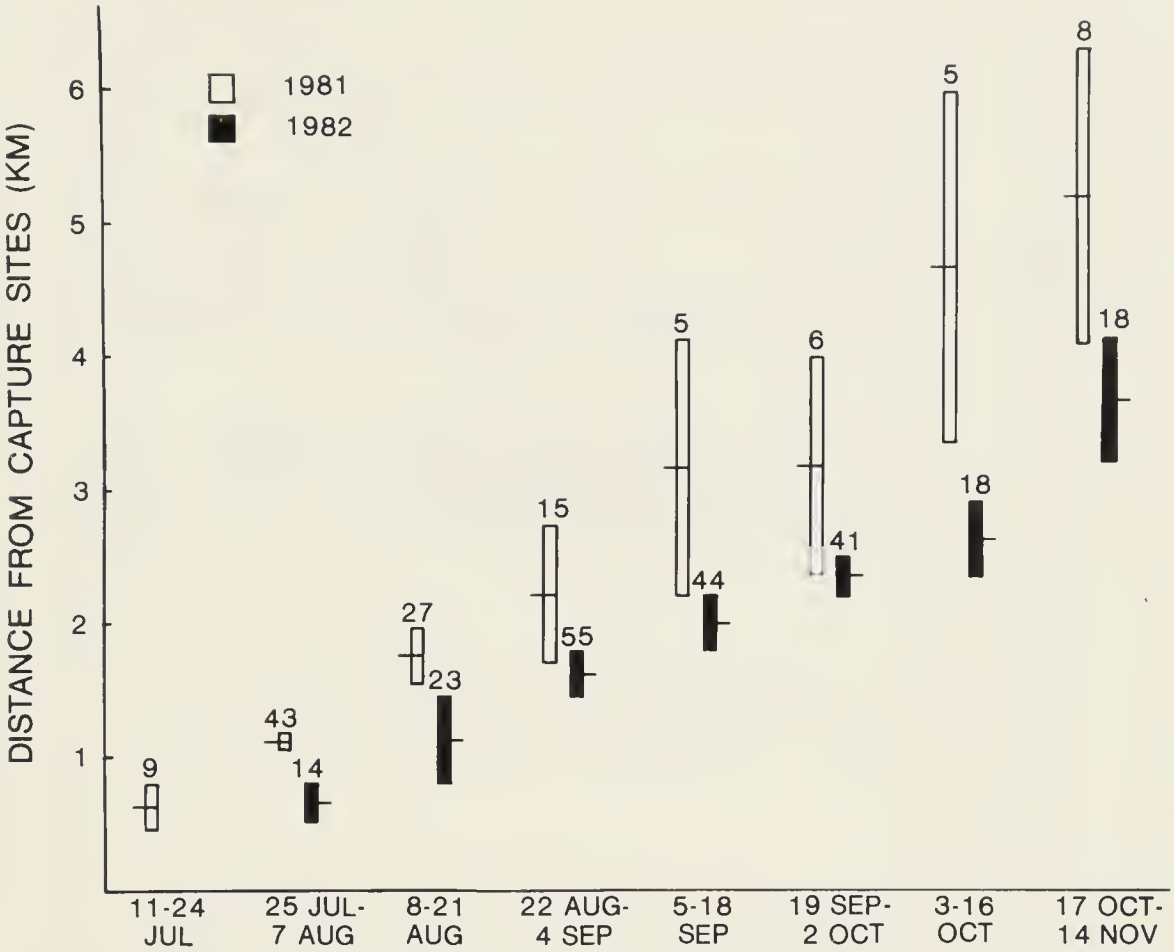


FIG. 1. Distance (km) moved from capture sites by 8 radio-marked Sage Grouse in 1981 and 10 grouse in 1982 on Cold Spring Mountain, Colorado. Horizontal line is the mean. The bar is one SE above and below the mean. The number above the bar is the number of radiolocations. Data are from 12 males and 6 females (Table 1).

to 14 November 1981 and 1982, 77 and 78%, respectively, of all radiolocations (10/13, 28/36) were >2 km from capture sites. In 1981, females were farther, on average, from their capture sites than males on any date after 10 August, while in 1982 males were farther, on average, from capture sites than females on any date after 1 August.

Movements of all but 3 (N = 18) birds in 1981 and 1982 had a nonrandom orientation, or significant mean direction, from capture sites (Rayleigh's test, $P < 0.00$) (Fig. 2). There was no significant mean direction when individual means of all birds were combined (Mardia's correlation coefficient, $P > 0.05$). Although we violated the test restriction that N should be equal for all birds, a slight variation of N has little effect on the statistical analysis (Batschelet 1978:6). Also, there was no obvious difference between directions of movements of males and females (Fig. 2). Males and females did not differ in mean direction moved in either year (Mardia-Watson-Wheeler test, $P > 0.05$).

Except for one male grouse (#501) found on Cold Spring Mountain on

TABLE 1

$R^2$ AND PROBABILITY ($P$)[a] OF SIMPLE AND MULTIPLE REGRESSION MODELS OF SAGE GROUSE DISTANCES FROM CAPTURE SITES (KM) WITH MOVEMENT RATE FROM PREVIOUS LOCATIONS (M/DAY), DATE, AND AGE OF BIRD ON COLD SPRING MOUNTAIN, COLORADO, 15 JULY–14 NOVEMBER 1981 AND 1 AUGUST–14 NOVEMBER 1982

| | | | | Distance from capture sites, $R^2$ ($P$) | | | | |
|---|---|---|---|---|---|---|---|---|
| Year | Bird | Sex | No. locations | Movement rate | Date | Age | Best multiple model[b] | Variables in multiple model |
| 1981 | 438 | M | 14 | 0.01 (>0.5) | 0.22 (0.25) | 0.22 (0.25) | None | None |
| | 465 | F | 10 | 0.01 (>0.5) | 0.77 (0.00) | 0.77 (0.00) | 0.77 (0.00) | Date or age |
| | 486 | M | 16 | 0.01 (>0.5) | 0.76 (0.00) | 0.64 (0.00) | 0.76 (0.00) | Date |
| | 501 | M | 18 | 0.11 (0.30) | 0.38 (0.01) | 0.38 (0.01) | 0.38 (0.01) | Date |
| | 585 | F | 13 | 0.00 (>0.5) | 0.66 (0.00) | 0.66 (0.00) | 0.66 (0.00) | Date |
| | 687 | M | 11 | 0.00 (>0.5) | 0.56 (0.01) | 0.56 (0.01) | 0.56 (0.01) | Date |
| | 712 | F | 18 | 0.12 (0.4) | 0.75 (0.00) | 0.75 (0.00) | 0.75 (0.00) | Date |
| | 785 | M | 18 | 0.00 (>0.5) | 0.57 (0.00) | 0.57 (0.00) | 0.57 (0.00) | Date |
| All birds | | | 118 | | | | 0.44 (0.00) | Date |
| 1982 | 520 | M | 28 | 0.00 (>0.5) | 0.59 (0.00) | 0.60 (0.00) | 0.60 (0.00) | Age |
| | 562 | F | 18 | 0.48 (0.00) | 0.10 (0.20) | 0.08 (0.25) | 0.69 (0.00) | Movement rate, age |
| | 576 | F | 27 | 0.08 (0.15) | 0.34 (0.00) | 0.34 (0.00) | 0.34 (0.00) | Date or age |
| | 669 | M | 15 | 0.27 (0.04) | 0.37 (0.02) | 0.45 (0.00) | 0.78 (0.00) | Age, movement rate |
| | 694 | M | 21 | 0.06 (0.27) | 0.00 (>0.5) | 0.00 (>0.5) | None | None |
| | 702 | M | 22 | 0.14 (0.09) | 0.74 (0.00) | 0.73 (0.00) | 0.74 (0.00) | Date |
| | 712 | F | 17 | 0.02 (>0.5) | 0.67 (0.00) | 0.67 (0.00) | 0.67 (0.00) | Date or age |
| | 734 | M | 15 | 0.04 (0.47) | 0.56 (0.00) | 0.56 (0.00) | 0.56 (0.00) | Date or age |
| | 757 | M | 28 | 0.02 (>0.5) | 0.56 (0.00) | 0.56 (0.00) | 0.56 (0.00) | Date or age |
| | 797 | M | 22 | 0.02 (>0.5) | 0.10 (0.16) | 0.09 (0.16) | None | None |
| All birds | | | 213 | | | | 0.59 (0.00) | Date, movement rate |

[a] Probability of no relationship between distance from grouse capture sites and the independent variable.
[b] Stepwise multiple regression.

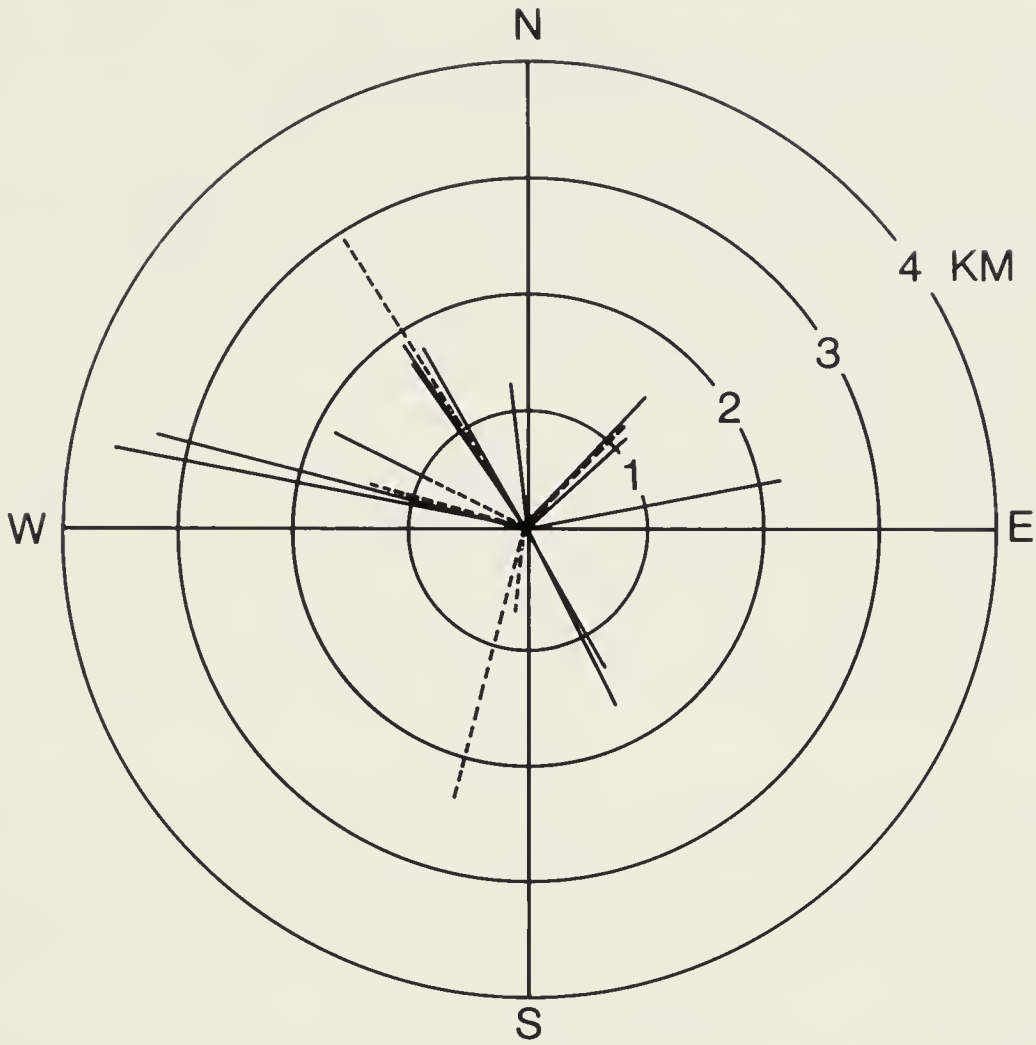


FIG. 2. Mean angles and mean distances (km) moved from capture sites of radio-marked juvenile Sage Grouse (N = 18) on Cold Spring Mountain, Colorado, July–November 1981 and August–November 1982. Solid lines are males (N = 12); dashed lines are females (N = 6).

21 January 1982, the last two radiolocations of juvenile grouse marked in 1981 were on 14 November. Male #501 and 35 other grouse were located in exposed sagebrush on 21 January 1982, but grouse were not seen after 2 Februray following a snowstorm that covered all exposed sagebrush. In fall 1982, 7 grouse were radiotracked until 14 November. One radio-marked adult hen was located on its wintering area 5 km northeast of Cold Spring Mountain on 15 December 1982. A juvenile male (#734, Fig. 3), which was radiotracked from August to November 1982 and January to May 1983, moved to its subsequent wintering area during 23–30 October 1982. The number of radio-marked grouse with known locations in 1982 decreased from 17 on 30 October to 7 on 14 November and to none on 25 November. During this period snow levels on Cold Spring Mountain increased from 0–5 to 20–50 cm. By 14

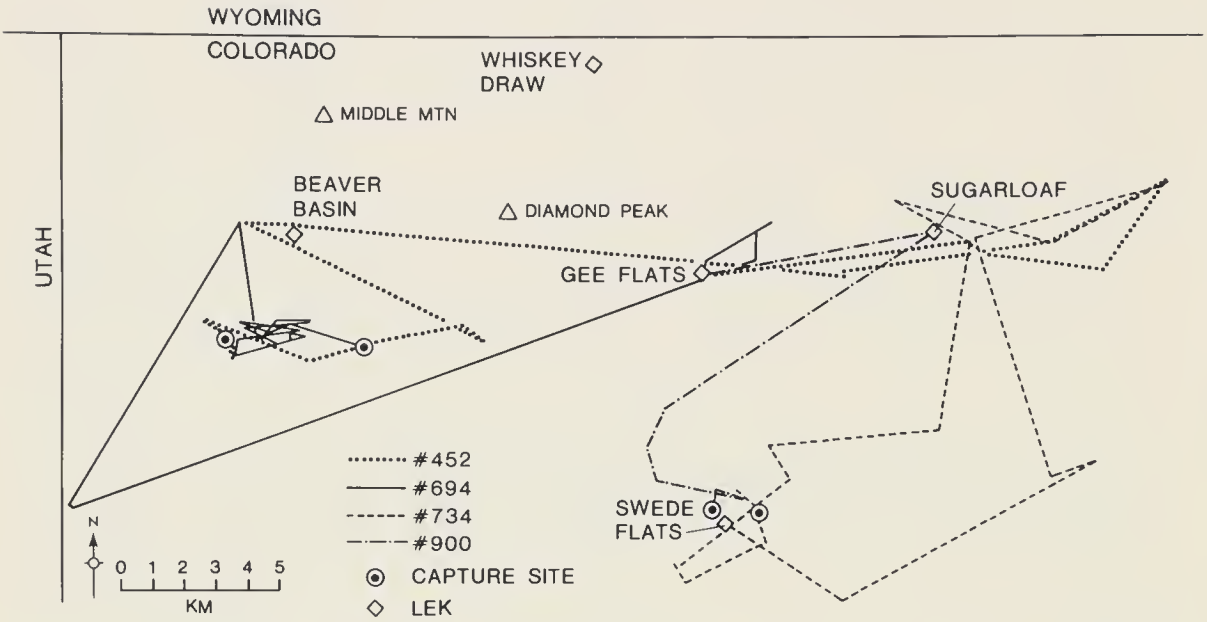


FIG. 3. Summer to spring movements of 4 radio-marked juvenile Sage Grouse (3 males; 1 female, #452) on Cold Spring Mountain, Colorado, 9 August–28 May 1982–83.

December, snow depth was ≥1 m and all sagebrush on Sage Grouse summer range was covered. Some birds appeared to leave summer range in late October–November, as 9 of the original 58 radio-marked grouse were lost prior to 3 October. None of these birds was later relocated, so we do not know if they were dispersing earlier than other grouse or whether there were other reasons for loss of radio signals. However, 4 of the 9 birds had moved ≥3 km when they were lost.

Four juveniles (3 males, 1 female) radiomarked in summer 1982 were located in January and February 1983 after being lost during late-November to mid-January. Maximum distance from capture sites to their locations in January–April 1983 averaged 18.2 km for these 4 birds. The female grouse moved a maximum of 30.3 km from her capture site, while the 3 males moved from 11.4 to 17.3 km from their capture sites (Fig. 3). Color-banded and radio-marked grouse were found wintering in two areas: one area was a 200-km$^2$ sagebrush flat 5–30 km northeast of Cold Spring Mountain; the other area (25 km$^2$) was 7 km southwest of Cold Spring Mountain along the Utah-Colorado boundary (Fig. 3). A radio-marked male (#694) in the latter wintering area moved 23 km to the wintering area northeast of Cold Spring Mountain between 2 February and 26 March 1983 and attended Gee Flats Lek, in the same area, from 4 April to 19 May (Fig. 3).

During the spring breeding season, all 4 radio-marked yearlings were observed on leks; however, male #734 appeared to spend most of the breeding season away from known leks. Male #734 and 6 other males were seen displaying near 3 females on the morning of 10 April, approx-

imately 2 km east of Sugarloaf Lek, and were again seen displaying on 14 April about 9 km southeast of Sugarloaf Lek. These areas were checked on six mornings, but no grouse were observed displaying regularly within 300 m of the initial locations. We did not observe male #734 on a known lek until late in the breeding season when it displayed on Swede Flats Lek on 25 May (Fig. 3). The 2 other radio-marked males spent totals of at least 22 and 9 days displaying on known leks. Female #452 was located approximately 1 km southeast of Sugarloaf Lek on four mornings during 3–10 April and on Gee Flats Lek on six mornings during 21–27 April. On mornings when female #452 was located with other females 1 km southeast of Sugarloaf Lek, groups of 5–6 males displayed nearby and followed the females through the sagebrush; the locations of these males were not considered leks because they moved daily. These observations suggest that there are roving groups of males, probably yearlings, that spend much of the breeding season displaying near females away from traditional lek sites.

## DISCUSSION

Late summer movements of juvenile Sage Grouse on Cold Spring Mountain were not characterized by rapid, synchronized movements by most members of the population, as Godfrey and Marshall (1969) found for Ruffed Grouse (*Bonasa umbellus*). Instead, movements of both sexes on Cold Spring Mountain were sporadic throughout September and October, similar to those reported for Greater Prairie-Chickens (Bowman and Robel 1977) and Sage Grouse in Idaho (Dalke et al. 1963). Movement rates on Cold Spring Mountain did not change during September–November because movements of >2 km were quick (about 1 day) and separated by periods of up to 20 days when birds did not move >0.3 km/day. We were unable to determine if there was a difference in movements between male and female Sage Grouse; however, no difference between the sexes was suggested by the longer movements of females than males in 1981 and the reverse in 1982.

Sage Grouse tended to follow topographic features and avoided areas without sagebrush cover, as mean angles of summer movements were generally along the northwest to southeast orientation of Cold Spring Mountain and away from its steep (80% slope) southwest face which was covered with pinyon-juniper forest. Sage Grouse, however, may cross large areas without cover as did radio-marked male #694, which crossed Cold Spring Mountain when all sagebrush on the mountain was snow covered.

Synchronized, long-distance movements to winter range may have occurred during mid-November to mid-January as locations of most radio-

marked birds were unknown during that time. Field observations indicated that Sage Grouse generally moved north to sagebrush flats and lower valleys as snow levels increased in November. Patterson (1952), Dalke et al. (1960), and Schoenberg (1982) reported that Sage Grouse movements between wintering and breeding (leks and nesting sites) areas were related to snow level and its effect on the availability of sagebrush. Movement distances probably varied depending on the distance to suitable cover above snow. Patterson (1952) and Dalke et al. (1960) reported one-way movements from summer to winter ranges of up to 160 km in Wyoming and Idaho, respectively. In Colorado, winter to breeding range distances averaged 28–30 km for 7 radio-marked grouse (4 females, 3 males) (Schoenberg 1982) and 8–12 km for color-banded grouse (68 males, 10 females) traveling from breeding to winter ranges (Beck 1977).

Another study of fall movements of radio-marked Sage Grouse (both adults and juveniles were tracked until 30 November) found that grouse generally left summer range in October and November (Connelly and Markham 1983). From 10 July to 7 September, 95% of all radiolocations (N = 131) in the Idaho study were $\leq 2$ km from the general capture area, while 82% of all locations (N = 22) were $>2$ km during October to November. These findings are consistent with results from Cold Spring Mountain. Three of 14 radio-marked grouse in Connelly and Markham's (1983) study moved from summer range prior to mid-September, while most birds did not leave until after 1 October.

During summer 1982, one yearling female and at least 2 chicks may have exhibited posthatching emigration as described by Watson and Moss (1980). From hatching during 25–27 June until 7 August, the hen and chicks were $\leq 2.5$ km from the nest site. On 7 August the female and chicks (45–47 days old) were 5.2 km from the nest site; the next day they were 9.6 km from the nest. The female was last seen with a chick on 17 August and had started moving back towards the nest site on 12 September. The hen was last located 2.2 km from the nest site on 3 October. In contrast, one other radio-marked female with a brood remained within 2 km of her nest site until loss of the radio transmitter on 8 August, and one of her chicks, which was radio-marked, did not move $>2.1$ km from the nest site until 12 September. Among 7 radio-marked females which were unsuccessful nesters, maximum distance from nests averaged 3.8 km prior to 20 August (range 1.3–6.5 km). Early dispersal or posthatching emigration may increase a yearling's chances of recruitment if there is a lower probability of establishing a territory in natal than in other areas.

During spring recruitment in lek species, it appears that some yearling males may only display infrequently on leks, or not at all. Robel (1969, 1970) observed radio-marked yearling Black Grouse (*Lyrurus tetrix*) and

Greater Prairie-Chickens that rarely attended leks, and Lill (1974) has described male White-bearded Manakins (*Manacus manacus*) engaged in courtship behavior away from leks. Similar evidence for a subpopulation that does not attend leks comes from a removal experiment with Sharp-tailed Grouse (*Tympanuchus phasianellus*) in which grouse recruited onto removal leks were probably nonterritorial yearlings (Rippin and Boag 1974). It may be advantageous for yearlings to postpone territory establishment on a lek until later years if territories which might lead to high mating success cannot be acquired easily during their first spring, as has been suggested for Blue Grouse (Lewis and Zwickel 1982, Jamieson and Zwickel 1983b).

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## ERRATA

In "A list of birds and their weights from Saul, French Guiana" by James A. Dick, W. Bruce McGillivray, and David J. Brooks (Wilson Bull. 96:347–365, 1984); paragraph 7 on page 355 should be deleted, as the wet specimen identified as a Tiny Tyrant-Manakin was determined to be a White-fronted Manakin (*Pipra serena*). On page 358, Bicolored Conebill . . . should read "White-shouldered Tanager (*Tachyphonus luctuosus*).—A wet specimen in juvenal plumage (KU 73387) 12 g, 17 February 1977, subsequently identified by Dr. K. C. Parkes." On page 359, under the heading "Conclusions and Summary" the last two lines of the first paragraph should read "Two species were reported in French Guiana for the first time. They were: *Neochelidon tibialis* and *Vireo altiloquus*." On page 363 under the heading "Appendix," line 21 should be deleted. On page 364, *Conirostrum bicolor* should read "*Tachyphonus luctuosus*."

*Wilson Bull.*, 98(1), 1986, pp. 93–100

# ASSORTATIVE MATING AND SEXUAL DIMORPHISM IN THE COMMON TERN

MALCOLM C. COULTER[1]

ABSTRACT.—Although male and female Common Terns (*Sterna hirundo*) are almost identical in plumage and in most external body measurements, males have longer, deeper, and wider bills than do females. Two patterns in the size relationships between mates are demonstrated. First, males tend to have larger bills than their mates. This may be explained by random mating, given the sexual dimorphism observed. Second, Common Terns mate assortatively according to bill size. This pattern may result if there is either a year-to-year component or an age component of bill size variation and if first-breeding birds return to the colony after experienced breeders have already established pairbonds and most birds retain their mates from year to year. *Received 11 Jan. 1985, accepted 30 Aug. 1985.*

Mating patterns may contribute significantly to the genetic structure of bird populations. When similar individuals tend to mate with each other (i.e., mating is positively assortative), progeny are more homozygous, and phenotypic variability in the population may be greater than when mating is either random or disassortative (Falconer 1981, Halliday 1978, Partridge 1983; but see Lande 1977). Positive assortative mating based on the color morphs has been demonstrated for white and blue morphs of the Snow Goose (*Chen caerulescens*) (Cooke et al. 1976). This involved discrimination according to a discrete variable (i.e., distinct blue and white morphs). It is more difficult to demonstrate mating patterns according to continuous variables, particularly in wild populations. Recently, Boag and Grant (1978) presented evidence that Medium Ground Finches (*Geospiza fortis*) mate assortatively according to bill size and tarsus length. In this paper I examine assortative mating and mating pattern according to size in the Common Tern (*Sterna hirundo*). Sexual dimorphism has not been demonstrated for Common Terns, although in two early works it was suggested that females tend to be slightly smaller than males (Coues 1903, Ridgeway 1919). I examine sexual dimorphism and ask whether the observed mating patterns may be due to random mating alone, given the sexual dimorphism observed.

## METHODS

I caught Common Terns, including both members of 61 pairs, on Great Gull Island, Long Island Sound, New York, in 1978, 1979, and 1980. For each individual, I measured wing length to the nearest mm. I also measured tarsus and middle toe length as well as culmen

[1] Savannah River Ecology Lab., P.O. Drawer E, Aiken, South Carolina 29802.

TABLE 1
BODY MEASUREMENTS OF COMMON TERNS CAUGHT ON GREAT GULL ISLAND IN 1978 AND 1979

| Body measurement | Sex | N | Mean | Standard deviation | Range | Probability of a difference between the sexes[a] |
|---|---|---|---|---|---|---|
| Weight (g) | Female | 55 | 117.0 | 7.88 | 102.8–134.7 | NS[b] |
| | Male | 50 | 117.1 | 7.02 | 104.1–138.5 | |
| Wing (mm) | Female | 55 | 268.1 | 5.08 | 258.0–284.5 | NS |
| | Male | 50 | 268.1 | 5.88 | 258.0–280.0 | |
| Tail (mm)[c] | Female | 30 | 148.4 | 7.53 | 132.0–169.0 | NS |
| | Male | 26 | 250.6 | 5.74 | 133.0–161.5 | |
| Tarsus (mm) | Female | 55 | 24.1 | 0.90 | 22.30–25.98 | NS |
| | Male | 50 | 24.0 | 0.76 | 22.55–26.06 | |
| Middle toe (mm) | Female | 55 | 24.0 | 1.24 | 20.85–26.45 | NS |
| | Male | 50 | 24.4 | 1.31 | 21.11–27.05 | |
| Bill length (mm) | Female | 55 | 34.7 | 1.50 | 30.95–37.85 | <0.001 |
| | Male | 50 | 37.0 | 1.42 | 34.32–41.00 | |
| Bill depth (mm) | Female | 55 | 8.0 | 0.48 | 6.85–9.27 | <0.001 |
| | Male | 50 | 8.4 | 0.34 | 7.54–9.19 | |
| Bill width (mm) | Female | 55 | 5.4 | 0.51 | 4.42–7.54 | <0.05 |
| | Male | 50 | 5.6 | 0.48 | 4.55–6.91 | |

[a] *t*-test.
[b] $P < 0.10$.
[c] Data from 1979 only.

length, depth, and width with either of two calipers. One caliper measured in metric to the nearest 0.05 mm; the other measured in English measurements to the nearest 0.001 in., from which the measurements were converted to the metric equivalents. I weighed birds to the nearest 0.1 g. In 1979 and 1980, I also measured tail length to the nearest mm. Through the efforts of the Great Gull Island Project, all of the birds were color-banded previously. Their sexes were determined by observing behavior during copulation. I examined the measurements for sexual dimorphism and assortative mating by relative size. Among the measurements I took, mating patterns were only discernible according to the bill measurements. In this paper I discuss only the patterns according to culmen length, but the same trends held for all culmen measurements (Table 3). In order to distinguish whether the observed mating pattern was due to random mating or to some other factor, I ran 25 simulations. In each simulation I paired the 61 females with the 61 males. I compared the mating patterns according to the body measurements in these random matings with the field data.

## RESULTS

*Sexual Dimorphism.*—Adult male and female terns are not morphologically distinct. Plumages are similar, and measurements for most body parts are not statistically different (Table 1). Averages for bill measure-

TABLE 2

STANDARDIZED COEFFICIENTS OF THE DISCRIMINANT FUNCTION FOR SEPARATING THE SEXES OF COMMON TERNS OF GREAT GULL ISLAND, LONG ISLAND SOUND, NEW YORK, IN 1978

| Body parts included | Standardized coefficients for three functions | | |
|---|---|---|---|
| | A | B | C |
| Bill length | −0.912 | −0.947 | −0.904 |
| Bill depth | −0.396 | −0.451 | −0.418 |
| Bill width | −0.013 | 0.082 | 0.144 |
| Weight | | 0.360 | 0.352 |
| Wing length | | | 0.082 |
| Tarsus | | | −0.225 |
| Middle toe | | | 0.074 |
| Accuracy of determination[a] | 72% | 80% | 80% |

[a] Percent of cases for which sex is correctly determined.

ments were different, although there were overlaps: 70% for culmen length, 91% for culmen depth, and 99% for culmen width. Based on these three measurements, one can accurately determine sex 72% of the time using discriminant function analysis (Table 2). If weight, a measure of body size, is included in the analysis the accuracy of statistical prediction increases to 80%. The discriminant function is D = 0.4647 (Bill length) + 0.3895 (Bill depth) − 0.1349 (Bill width) − 0.0485 (Weight) − 17.1862, where culmen length, depth, and width are in mm; weight is in g; and D < 0.00 for females and >0.00 for males. Accuracy is not increased further by including additional body measurements. For a given body size, males have larger bills than females. These findings are not surprising: a combination of head and bill length is sufficient to determine sex in a number of species of gulls (Larinae) (Coulson et al. 1983).

*Mating Pattern.*—Within pairs of Common Terns, there was no tendency for individuals of one sex to be larger than those of the other sex, except in bill size (Table 3). In 60 of 61 pairs, males had longer bills than their mates (Sign Test, $P < 0.005$). In the exceptional pair, the female's bill was 0.11 mm longer than her mate's bill, a difference within measurement error. The average difference in bill length was 2.60 mm ± 1.48 (SD). At the same time, mating was assortative: males with longer bills tended to mate with long-billed females, and short-billed males tended to mate with short-billed females. The correlation coefficient between males and females of individual pairs was $r = 0.46$ (N = 61, $P < 0.05$) (Fig. 1). Correlation coefficients for other body parts between mates were not significant. Assortative mating according to bill length and whether

TABLE 3

BILL SIZE DIFFERENCES BETWEEN SEXES WITHIN PAIRS OF COMMON TERNS ON GREAT GULL ISLAND, LONG ISLAND SOUND, NEW YORK

| Bill measurement | Males larger than females | Males and females the same size | Females larger than males | Probability of a significant difference[a] |
|---|---|---|---|---|
| Length | 60 (98)[b] | 0 (0) | 1 (2) | $\ll 0.0001$ |
| Depth | 49 (80) | 1 (2) | 11 (18) | $\ll 0.001$ |
| Width | 42 (69) | 2 (3) | 17 (28) | $=0.002$ |

[a] Two-tailed sign test.
[b] N (%).

males have longer bills than their mates are distinguishable, and I deal with this below.

## SIMULATION OF MATING PATTERNS

An observed mating pattern may be due to any of a number of factors: discrimination among potential mates, annual variation in adult size coupled with mating predominantly among cohorts, or even random mating in sexually dimorphic species. Common Terns are sexually dimorphic according to bill size. It is important, therefore, to distinguish whether the observed mating pattern may have been due to random pairing alone, or whether some other factors such as distinguishing among potential mates may also have been involved. To examine the importance of random pairing, I paired, according to a random number table, the 61 members of each sex in 25 simulations. I compared the bill lengths among pairs obtained by this simulation with the measurements of bill lengths for the pairs that I collected in the field. I asked three questions:

(1) Can random mating alone explain the high proportion of pairs in which males have longer bills? One would expect, given the sexual dimorphism observed, that under random mating alone there would be a large number of pairs in which the males had longer bills than their mates. In 25 random simulations, males had longer bills in an average of 56 pairs (92%). This was not significantly different from the 60 out of 61 pairs observed in nature (Fisher's Exact Test, $P = 0.090$). It is possible that Common Terns choose their mates so that males have longer bills and that only a very large sample size would demonstrate a difference from the 92% of the pairs with males having longer bills that would be expected under random mating. The only exceptional case observed in this study involved birds whose bills were, within measurement error, almost identical. At present, however, random mating is sufficient to explain this pattern.

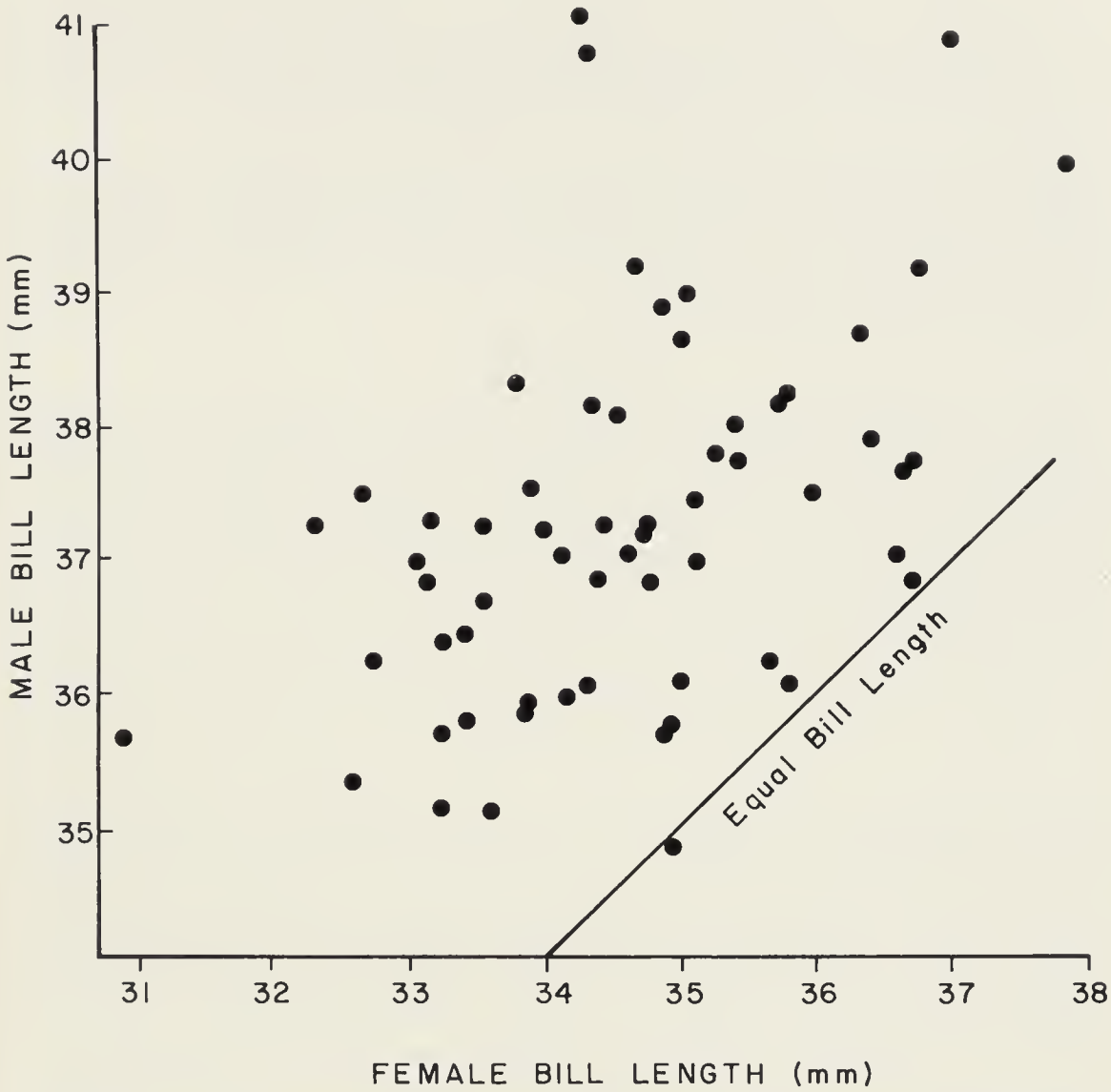


FIG. 1. Relation of culmen lengths of pairs of Common Terns caught on Great Gull Island.

(2) Can random mating alone explain the assortative mating? The correlation between bill lengths of mates was significant. This indicated that the assortative mating observed was not the result of random pairing. Furthermore, among the 25 random pairings, none was significant (range of correlation coefficients: $-0.215$ to $+0.298$, $P > 0.05$). Random mating, then, would not lead to a pattern of assortative mating.

(3) Can the observed pattern of males having longer bills than their mates explain the assortative mating? Among the 25 random trials, when I considered only those pairs in which males had longer bills, I found that in all but one of the trials the correlation coefficients were not significantly different from zero ($P > 0.10$); in the one case the coefficient was 0.401 ($P < 0.05$). The average correlation

coefficient ($r$) for the 25 trials was 0.09, significantly less than the 0.46 observed. Thus, the pattern of males having longer bills than their mates cannot explain the assortative mating.

The results of the simulation indicate that random mating is sufficient to explain the high frequency of pairs in which the males had longer bills than their mates. However, random mating would not lead to the positive assortative mating observed.

## DISCUSSION

I have demonstrated two patterns in the size relationships between mates of Common Terns: (1) assortative mating and (2) that males have larger bills than their mates. These patterns seem to be independent from each other and so may be due to different factors. I discuss them separately.

*Males have larger bills than their mates.*—A difference in bill size between mates has been shown for other members of the Charadriiformes. Among some species of shorebirds, females tend to be larger than males, and in those species examined the females had larger bills in nearly all pairs (Harris 1967, Jehl 1970, Soikkeli 1966). In many gull species, males tend to be larger than females. Harris and Hope-Jones (1969) examined bills in pairs of Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*L. fuscus*) and found that in almost all pairs the male had the larger bill. All of these species show sexual dimorphism in bill size, and random mating alone may explain the size relationships between mates. Random mating is sufficient to explain this pattern in Common Terns.

*Assortative mating according to bill size.*—The case for Common Terns described here is the first demonstration of assortative mating according to a nondiscrete character for any Charadriiformes species. Halliday (1978) has suggested that assortative mating according to a nondiscrete character would maintain greater phenotypic variability than would be found under other mating patterns. Lande (1977), however, developed a model that indicated that when mutation and selection are considered for a large population, the mating pattern would have no influence on genetic variability in the population. We can differentiate between these two hypotheses because they predict different shapes of the statistical distribution of the character involved. According to the former approach, one would expect a platykurtic distribution (i.e., the tails of the distribution would have more observations than if the measurements were normally distributed); according to Lande's approach, one would expect a normal distribution, which is what I found ($\gamma_1 = 0.393 \pm 0.330$ (SD), $P > 0.10$; $\gamma_2 = 3.235 \pm 0.661$ (SD), $P > 0.10$).

Nisbet et al. (1984) have shown that Common Terns mate assortatively

according to age. The factors that led to the assortative mating are not apparent. Coulson and Thomas (1983) have demonstrated that Black-legged Kittiwakes (*Rissa tridactyla*) also mate assortatively according to age. First-breeding birds usually pair together because they arrive at the colony late, at which time most of the experienced breeders have already established pairbonds. Many birds retain their mates from year to year. A similar pattern may also exist among Common Terns. At the same time, there may be a year-to-year component of bill size variation. Year-to-year variation in tarsus length has been demonstrated for the Great Tit (*Parus major*) (Garnett 1981). Alternatively, if bills grow slowly after fledging and during the first few years of adult life, then this may impose an age component to bill size variation. Slow growth of adult Herring Gull bills has been demonstrated by Coulson et al. (1981). If, then, there is a tendency for Common Terns to mate assortatively according to age, and if either (1) there is a year-to-year component of bill size variation or (2) there is an age component of bill size variation, then this may explain the assortative mating according to bill size.

## ACKNOWLEDGMENTS

I am thankful to the Frank M. Chapman Memorial Fund for a fellowship that supported this study, and I am grateful to Helen Hays for permission to work on Great Gull Island and for providing facilities on the island. I thank the Long Point Bird Observatory and the Savannah River Ecology Laboratory for providing a place to write. Preparation of this manuscript was supported by contract DE-AC09-76SR00-819 between the University of Georgia's Savannah River Ecology Laboratory and the U. S. Department of Energy. A. Brash, D. Evans, and E. Liebson helped with measurements in the field. J. Novak provided advice on statistics. L. Orebaugh drew the graphics. I thank R. Banks, G. Barrowclough, J. Burger, C. Collins, J. DiCostanzo, J. Farrand, Jr., P. Grant, J. Greenway, H. Hays, M. LeCroy, R. J. O'Connor, R. Payne, A. Poole, T. Price, R. E. Ricklefs, and F. Vuilleumier for discussions and comments on earlier versions of the manuscript. This is contribution number 64 of the Great Gull Island Project.

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## GENERAL MEETING
## OF THE WORKING GROUP ON GRANIVOROUS BIRDS—INTECOL

On 13 August 1986, during the meeting of the IV International Congress of Ecology, Syracuse, New York, USA, 10–16 August 1986, the General Meeting of the Working Group on Granivorous Birds—INTECOL, will be held.

The theme of the symposium has been tentatively formulated as "The role of granivorous birds in ecosystems." The following topics will be included: (1) population dynamics, (2) biomass and production rates, (3) energetics, (4) impact of granivorous birds on ecosystems, and (5) pest management.

The symposium will include a review of up-to-date results of international studies on certain granivorous birds and a discussion of the most fruitful directions for further study.

Oral presentations at the symposium will be limited to 15 min. The program of the symposium will be established by 31 December 1985, based on titles and one-page abstracts submitted by that date.

All correspondence including requests for information should be sent to: Chairman of Working Group—Professor Dr. Jan Pinowski, Dept. Vertebrate Ecology, Institute of Ecology/PAS, Dziekanow Lesny, 05-092 Lomianki, Poland.

*Wilson Bull.*, 98(1), 1986, pp. 101–109

# RUDDY TURNSTONES, GREAT HORNED OWLS, AND EGG LOSS FROM COMMON TERN CLUTCHES

RALPH D. MORRIS AND DAVID A. WIGGINS[1]

ABSTRACT.—In two successive years, eggs of Common Terns (*Sterna hirundo*) disappeared or were found freshly perforated only from clutches initiated relatively early in the breeding season. Most of the losses were of single eggs from which an incubating adult was temporarily absent. Diurnal dreads of adult terns coincided with evidence of nocturnal predation by Great Horned Owls (*Bubo virginianus*). Ruddy Turnstones (*Arenaria interpres*) were observed breaking open and eating the contents of Common Tern eggs. We consider various explanations of the timing and pattern of egg loss. Circumstantial evidence supports the suggestion that nocturnal disturbance by owls at a time when Ruddy Turnstones are present at the colony may increase the risk of daytime predation by turnstones on tern eggs. *Received 10 Apr. 1985, accepted 21 Oct. 1985.*

The two principal nocturnal avian predators of Common Terns (*Sterna hirundo*) in North America are Black-crowned Night-Herons (*Nycticorax nycticorax*), which consume eggs and chicks (Collins 1970, Hunter and Morris 1976), and Great Horned Owls (*Bubo virginianus*), which prey upon chicks and adults (Nisbet 1975). Predation of tern eggs by Ring-billed Gulls (*Larus delawarensis*) occurs rarely (Courtney and Blokpoel 1980), whereas Herring Gulls (*L. argentatus*) have not been reported to consume tern eggs, although they sometimes prey heavily on chicks (Hatch 1970). Ruddy Turnstones (*Arenaria interpres*) eat eggs of several tern species (Crossin and Huber 1970, Loftin and Sutton 1979), including those of Common Terns (Parkes et al. 1971).

During four years of study at a colony of Common Terns in Lake Erie, the disappearance of eggs was responsible for from 18% (Morris et al. 1976) to 45% (Hunter 1976) of the total number of eggs that failed to hatch. Disappearance was most common during May, at the peak time of laying. As part of a larger study in 1982 and 1983, we obtained information on the timing and pattern of egg disappearance from Common Tern clutches, the eating of eggs by Ruddy Turnstones, and the association of these phenomena with probable predation by Great Horned Owls. We here report on these relationships.

## STUDY AREA AND METHODS

The tern colony was on an artificial breakwall, about one km off the north shore of Lake Erie near Port Colborne, Ontario (42°53′N, 79°16′W). Terns nested on a linear concrete

[1] Dept. Biol. Sci., Brock Univ., St. Catharines, Ontario L2S 3A1, Canada. (Present address DAW: Dept. Biol. Sci., Simon Fraser Univ., Burnaby, British Columbia, V5A 1S6 Canada.)

shelf (approximately 6 × 270 m) and traditionally have occupied the shelf area from west to east as the season progressed (Morris et al. 1976). One elevated observation blind was erected at the west end in front of an area (approximately 6 × 20 m) that was covered by a layer of soil overgrown by mossy stonecrop (*Sedum acre*). A second blind was about 100 m to the east in front of an area (approximately 6 × 30 m) containing gravel, logs, and plants that we had added to the existing concrete substrate (Richards and Morris 1984).

The study site was visited daily from 2 May to 16 July 1982 and from 1 May to 29 June 1983. We always approached each blind from the water and stepped onto the breakwall immediately behind it. Before entering the blinds, we marked new clutches with numbered wooden tongue depressors; eggs were marked soon after they were laid. Massed flights ("dreads") of all terns in the colony were frequent throughout May in both years (see below). Accordingly, to reduce the amount of time spent in the western study area during May, we obtained most information on the fate of eggs in clutches there by observation with binoculars from the blind. Vegetation growth was minimal early in the season, and the fate of eggs in many study clutches was readily followed by this procedure. Periodic nest checks were made to confirm the state of each clutch; we did not, however, take the extra time required to check hatching success of all clutches. Similar procedures were used to follow the fate of eggs in clutches initiated during late May, June, and July in the eastern study area. In addition, daily nest checks, made either after (morning) of before (evening) a blind watch, permitted a more detailed accounting of egg fate including hatching success.

In 1982, we made observations from both blinds each day during the 3 h following sunrise or the 3 h preceding sunset. In 1983, we were in both blinds for 8 h each day (4 h following sunrise and 4 h before sunset) until 14 May. Thereafter, daily observation periods of 3 or 4 h were made in each blind following sunrise or prior to sunset.

As one of several specific observations relating to a broader study of Common Tern behavior, we recorded the number of times that groups of terns simultaneously flew off their nests and the approximate percentage of all birds in the colony (total of 900–1000 pairs) that participated. We classified flights into two categories: those in which almost all birds departed virtually simultaneously ("dreads", Marples and Marples 1934), and those in which birds in only a small portion of the colony did so (hereafter called "up-flights"). Dreads were characterized by a sudden quietness in the colony followed by a departure of 90–100% of all terns in the colony. Up-flights were characterized by groups of terns in a small portion of the colony flying up and hovering a few meters above their clutches for brief periods of time before returning to incubate. Any obvious proximate stimulus associated with either type of flight was noted.

## RESULTS

*Diurnal tern flights.*—The patterns of dreads (major flights) and up-flights (minor flights) recorded in each year are shown in Fig. 1. In both years, the frequency of dreads gradually declined throughout the season with the exception of marked increases during mid-May (Fig. 1A). Most (>95%) dreads occurred without an obvious external stimulus; a few were preceded by a boat whistle or the approach of a fishing boat. During

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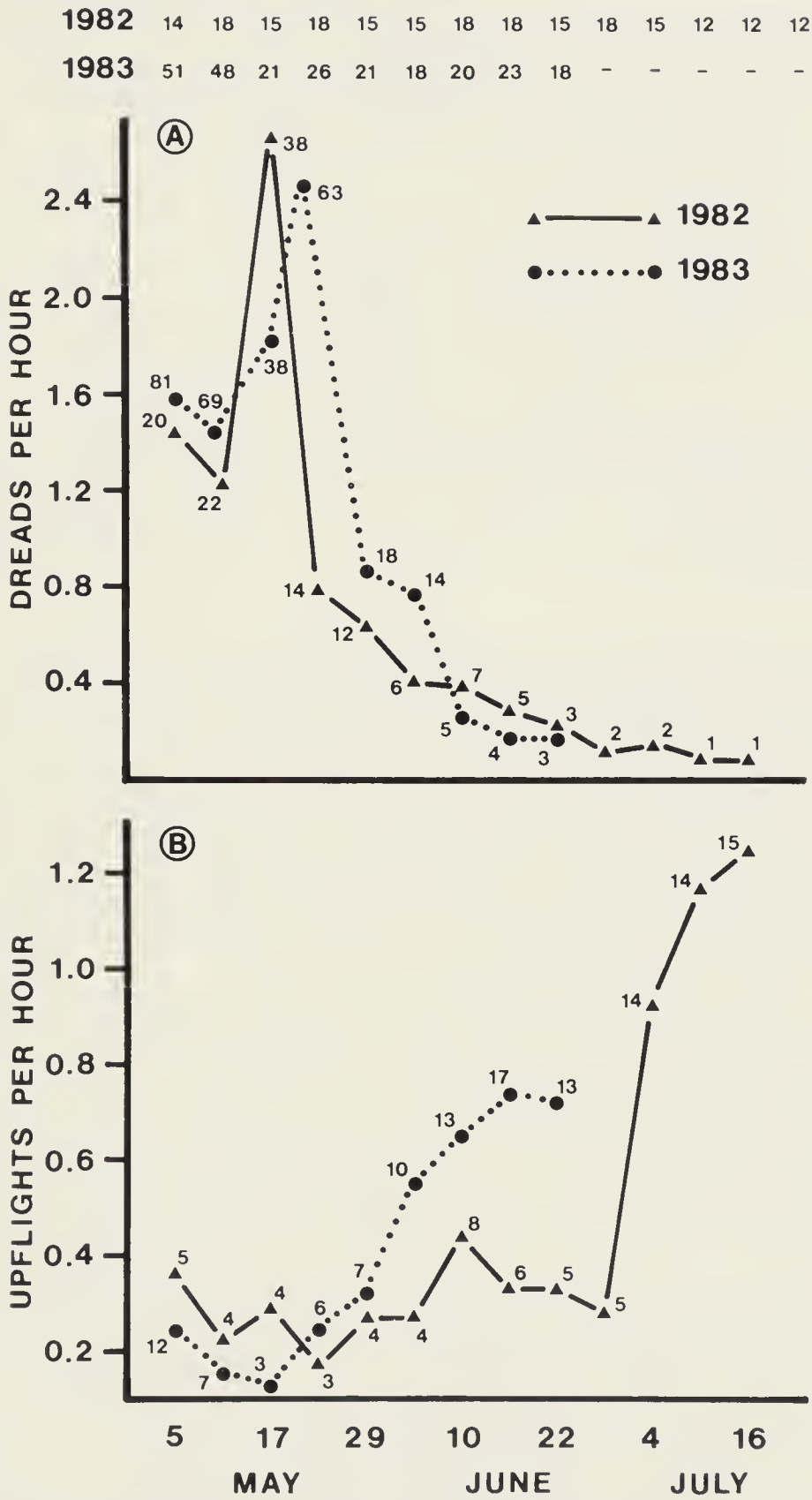
FIG. 1. Mean number of group flights per hour by Common Terns between 3 May and 16 July in each of two years. A. Major flights ("dreads") involved 90–100% of all terns in




the colony. B. Minor flights ("up-flights") were in response to a local disturbance (see text). The number of hours of observation during 6-day periods are shown across the top of the figure. Data points are connected by lines to aid the reader and do not imply interpolation.

TABLE 1
THE NUMBER OF EGGS THAT DISAPPEARED (N = 27) OR WERE FOUND FRESHLY PERFORATED (N = 15) WITHIN THE STUDY AREAS

| Year | Dates | No. clutches | Eggs present in scrape when loss occurred | | |
|---|---|---|---|---|---|
| | | | 1 | 2 | 3 |
| 1982 | 9–16 May | 117[a] | 10 | 3[b] | 4[c] |
| | 29 May–14 June | 96[a] | 12 | 3[d] | 6[e] |
| | 15 June–2 July | 65 | 0 | 0 | 0 |
| 1983 | 6–10 May | 34[f] | 4 | 0 | 0 |
| | 9–29 June | 25 | 0 | 0 | 0 |

[a] Four- and five-egg clutches not included.
[b] One egg from three clutches.
[c] Two eggs from two clutches.
[d] One complete clutch; one egg from another clutch.
[e] Two complete clutches.
[f] About 100 other clutches present; fate of eggs not followed.

dreads, all adult terns were absent from the colony for from 3 to 10 min, with the longer durations characterized by a low sweep of all birds over the colony, followed by a high aerial flight several hundred m south over Lake Erie. Dreads occurred 16 times during the morning watch of 17 May 1982, about 3 times more often than the average during the previous 15 daily observation periods. Dreads were again frequent (10 times during the 3-h period) during the next regular watch on the evening of 18 May. On 17 May we found the head of a Common Tern and a partially eaten carcass adjacent to the western study area. On 18 May, we walked the length of the breakwall and found two additional heads of terns and another partially eaten carcass with the head missing.

Up-flights occurred at a low frequency during May of both years and increased sharply thereafter (Fig. 1B). An obvious external stimulus always preceded these flights. In most cases (>95%) during late June and July, the stimulus was a recently fledged Ring-billed Gull which, upon landing on the breakwall, was immediately harassed by the adult terns closest to it. In other cases, up-flights were stimulated in a portion of the colony by a Herring Gull flying down to capture a Common Tern chick.

*The pattern and timing of egg loss.*—Within our study areas, 42 eggs disappeared shortly after they were laid, or were found freshly perforated; 32 of these (76%) were lost within 1–3 days of laying, and all were in scrapes containing 1 or 2 eggs (Table 1). The remaining 10 eggs disappeared from completed 3-egg clutches within 2–5 days of clutch completion (2 cases of 2 eggs lost; 2 cases of complete clutch loss). Egg loss due to disappearance or perforation was restricted to clutches initiated during

TABLE 2
THE FATE OF EGGS THAT FAILED TO HATCH FROM CLUTCHES IN THE EASTERN STUDY AREA[a]

| Year | Dates | Eggs hatched (% of egg pool) | Fate of egg: Disappeared/ perforated | Abandoned | Incubated to 21 days (unhatched) | Cracked | Unknown |
|---|---|---|---|---|---|---|---|
| 1982 | 29 May–14 June | 194 (78.9) | 21/6 | 8[b] | 15 | 3 | 5 |
| | 15 June–2 July | 143 (85.2) | 0 | 9[c] | 12 | 1 | 3 |
| 1983 | 9–29 June | 64 (88.8) | 0 | 8[d] | 0 | 0 | 0 |

[a] Hatching success of clutches visible from the blind in the western study area: 9–16 May 1982, 39 clutches, 102 of 116 eggs hatched (87.9%); 6–10 May 1983, 34 clutches, 77 of 93 eggs hatched (82.8%).
[b] Two 1-egg clutches; three 2-egg clutches.
[c] All 1-egg clutches.
[d] Four 1-egg clutches; two 2-egg clutches.

the 2 intervals prior to 14 June 1982, and to those initiated in the period 6–10 May 1983 (Table 1). Furthermore, eggs lost from scrapes containing a single egg at the time of loss were disproportionately overrepresented in both years. Of all eggs present in study clutches at the time of loss, a slightly higher proportion of eggs disappeared or were perforated in 1982 (38 of 532, 7.1%) than in 1983 (4 of 93, 4.3%). We contrasted the number of clutches that lost eggs with those that did not lose eggs, according to the clutch size at the time of loss. In both years, 1-egg clutches experienced significantly greater loss than 2-egg or 3-egg clutches (1982, $\chi^2 = 58.2$, df = 2, $P < 0.001$; 1983, Fisher's exact test, $P = 0.0002$).

In addition to egg losses within our study areas, we recorded 83 freshly broken Common Tern eggs during a systematic search through the colony on the morning of 18 May 1982. Most of these eggs were broken open and the contents partially drained; the remainder were intact except for a small puncture hole on the top surface. Several dozen scrapes were noted in which no eggs were present, but dried yolk stain was visible in the nest cup or around the scrape.

The more-frequent nest checks in the eastern study area permitted us to determine other probable causes of egg failure there (Table 2). Twenty-seven eggs were incubated for at least 21 days and failed to hatch. Most (21 of 27, 77.9%) were third-laid eggs in 3-egg clutches; the remainder were eggs in 2-egg clutches (N = 3) that failed to hatch. Abandoned eggs were observed in all time periods. Most (N = 15) were in scrapes that contained only a single egg; the remainder (N = 10) were in five 2-egg clutches.

*Ruddy Turnstone activity.*—Ruddy Turnstones were first seen at the

tern colony on 6 May 1982 and 9 May 1983; they were last seen on 12 June 1982 and 6 June 1983. These dates coincide with the usual timing of their northward migration each year in the eastern Lake Erie area (Buffalo Ornithological Society 1965). Flocks of 20–50 turnstones periodically congregated each day at loafing sites along the edge of the shelf, and on a rock pile near the water about 90 m to the west of the colony.

We recorded turnstones foraging individually or in small groups within our study areas on 14 occasions. Foraging behavior was characterized by rapid forward movement and periodic stops during which birds flipped over loose concrete chips and small rocks. Individuals restricted their activity to the edge of the colony and appeared hesitant to wander among incubating Common Terns. We observed turnstones cracking open tern eggs and eating the contents on six occasions. In five cases, the single egg in each of five scrapes was opened; in the remaining case, both eggs in a 2-egg clutch were opened. In each of these instances, an adult tern had been incubating the egg(s) within the few hours prior to loss to a turnstone. As the turnstone was undisturbed during the depredation event, we assume that the parents were not in the immediate vicinity of the nest during the attack (see below). The predator attacked the egg(s) with several sharp blows to the shell, opened a hole several cm in diameter, and consumed the contents, all within less than 60 sec. When uninterrupted, the turnstone ate all of the egg contents, leaving the empty shell(s). The shells were absent during our next visit to the colony, either on the day of loss or the day thereafter. Incubating tern parents adjacent to the egg-eating turnstone emitted a characteristic "churr" call at the intruder but did not chase it from the area. Foraging turnstones often oriented toward clutches that were unattended by either parent. In all but the six cases noted above, one or both parents were apparently present in the immediate area because an adult tern flew at the turnstone, which fled on foot. In all such cases, the attacking tern resumed incubation of the egg(s) after the turnstone left.

## DISCUSSION

The pattern and timing of loss for eggs that disappeared or were found freshly perforated indicate that single eggs laid early in the season were particularly vulnerable. Eggs disappeared or were perforated only during that portion of the breeding season when Ruddy Turnstones were present. In previous years at this colony, egg disappearance from early clutches has been a common type of egg failure (Hunter 1976, Morris et al. 1976, Courtney 1977). Eggs in early clutches are often incubated infrequently by adult terns during the first few days after laying (Courtney 1979); such eggs would be particularly susceptible to damage by turnstones. Finally,

we observed Ruddy Turnstones breaking open and eating Common Tern eggs that were temporarily left unguarded by the incubating parents. Thus, actual and circumstantial evidence implicates Ruddy Turnstones as predators of Common Tern eggs.

When eggs disappear or are found perforated, the agents of loss or damage are often enigmatic, and coincident events, while circumstantially related, cannot necessarily be taken as correlated. The number of times that we saw turnstones cracking eggs and consuming the contents was very few, and no egg-eating was observed early in the season when dreads were frequent. Egg predation by Ruddy Turnstones did not appear to be a problem at this colony in previous years, and H. Blokpoel (pers. comm.) has only recently (1983, 1984) noted turnstones damaging Common Tern eggs at a colony near Toronto, Ontario. I. Nisbet (pers. comm.) does not consider turnstones a significant egg predator in Common Tern colonies on the east coast. Therefore, we examined other biological factors that might have produced the particular pattern and timing of egg loss observed in 1982 and 1983.

We considered three possible alternatives. First, although it occurs only rarely, Ring-billed Gulls take the eggs of Common Terns (Courtney and Blokpoel 1980). Second, at Common Tern colonies on the east coast, egg perforation and breakage were higher in years where Great Horned Owl predation was suspected; egg damage was attributed to the terns themselves although no actual observations were made of the behavior (Nisbet and Welton 1984). Third, Black-crowned Night-Herons take Common Tern eggs and chicks at night (Hunter and Morris 1976). Such predation can be especially severe when owls cause terns to depart the colony (Nisbet and Welton 1984).

In 1985, we observed a single Ring-billed Gull take a Common Tern egg on several different occasions. A bird that we assumed to be the same individual walked several m away from its own clutch near the extreme western end of the tern colony, removed a single egg from a tern nest, and consumed it whole. In three previous years of intensive observation from blinds at this colony, we never saw a Ring-billed Gull take a Common Tern egg, and we assume the 1985 observations were unique. Once terns begin nesting, they experience little interference of any kind from Ring-billed Gulls nesting nearby (Morris and Hunter 1976, Courtney and Blokpoel 1980). We do not exclude the possibility that adult terns themselves caused damage to their eggs during the many resettling events following dreads throughout May in both years. The disproportionate loss of eggs from mostly incomplete clutches, however, is not consistent with terns causing the damage. Finally, Black-crowned Night-Herons stimulate nocturnal desertion by adult terns independently of the presence of owls

(Hunter and Morris 1976). In predation events seen at the Port Colborne colony, recently hatched chicks and late pipping eggs (eaten whole) were particularly vulnerable, as the heron, oriented by sound to the prey. Such directed selection of prey items is not consistent with our current observation that single eggs laid early in the breeding season were particularly vulnerable, especially in the first few days after they were laid.

Ruddy Turnstone predation of tern eggs can be severe under certain circumstances. Wetmore (in Bent 1929:288) noted that eggs of both Sooty Terns (*Sterna fuscata*) and Gray-backed Terns (*S. lunata*) on the Laysan Islands were at greatest risk when incubating terns were disturbed by investigator activity. Furthermore, terns on these islands apparently had a limited chance of nesting success until most turnstones had left the island in northward migration (Crossin and Huber 1970). Thus, of possible explanations for the egg losses observed at Port Colborne in 1982 and 1983, we suggest that predation by Ruddy Turnstones best accounts for both the pattern and timing observed. Although less likely to have been the principal cause, predation by Black-crowned Night-Herons may have contributed to the egg losses.

Nisbet and Welton (1984) noted numerous indirect negative effects of Great Horned Owl predation on Common Tern eggs and chicks. In both years of our study, dreads occurred throughout May with sharp peaks during the middle of that month. Conversely, upflights were restricted to late in the season, were clearly related to an immediate proximate disturbance, and involved only a small portion of all adult terns in the colony. We suggest that an increase in tern "flightiness" during diurnal periods (noted as an increase in the frequency of dreads) may be another indirect consequence of owl predation. The severed heads and dismembered bodies of adult terns found during our single check of the total colony implicate Great Horned Owls as the predator. We did not search for dead adult terns on other days as the disturbance caused by such investigator activity could not be justified. Accordingly, we recognize that we do not have firm evidence that the frequency of diurnal dreads was correlated with owl predation on previous evenings. However, coincidence in the timing of nocturnal disturbance by owls, and the diurnal presence of Ruddy Turnstones may increase the susceptibility of tern eggs to these egg predators. Such events are not expected to coincide in all years at all tern colonies. When they do, we predict the loss of Common Tern eggs in the pattern noted.

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# PREY-SIZE SELECTION IN NESTING MALE AND FEMALE COOPER'S HAWKS

PATRICIA L. KENNEDY[1] AND DONALD R. JOHNSON[1]

ABSTRACT.—The size and frequency of prey delivered by nesting Cooper's Hawks (*Accipiter cooperii*) were monitored throughout the nestling period at five nests on Lopez Island, Washington. Based on vocalizations during food exchange, we estimate that males captured 63% of the prey delivered to nests. Birds, primarily American Robins (*Turdus migratorius*) and California Quail (*Callipepla californica*), represented 85% of the prey captured by both males and females. The food niches of both sexes were similar as measured by maximum likelihood estimators of niche breadth and overlap. When the counts of prey delivered by males and females were adjusted for bias due to unequal observation time between years and differential hunting effort by the sexes, there were no significant differences between the sexes, nesting pairs, or prey size classes in the number of prey delivered to nests. These results and those of several other studies call into question the food-niche hypothesis as a comprehensive explanation for sexual size dimorphism found in many raptorial birds. *Received 26 Apr. 1984, accepted 25 July 1985.*

Several authors have proposed that sexual size dimorphism in raptors is advantageous because it allows prey-size partitioning between the sexes, and thus more efficient use of the food resource (Selander 1966, Storer 1966, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981). To test this hypothesis, we monitored the size of prey taken by five pairs of Cooper's Hawks (*Accipiter cooperii*) and compared the frequency of prey delivery based on prey size, nesting pair, and sex.

## STUDY AREA AND METHODS

The study was conducted on Lopez Island off the northwest coast of Washington, where Cooper's Hawks nest in the absence of Goshawks (*A. gentilis*) and Sharp-shinned Hawks (*A. striatus*). Because the diets and habitat use of these three species overlap in areas where they coexist (Reynolds et al. 1982, Moore and Henny 1983, Reynolds and Meslow 1984), the absence of interspecific competition on Lopez Island may permit a greater opportunity for segregation of the diets of the sexes.

The activities of five nesting pairs were observed from blinds for 4–16 h every third day from early June through fledging in mid-July, 1978–1979. Observations of a sixth pair were terminated in 1978 following loss of its five nestlings to owl predation. Data for this pair are excluded from our analysis. We have assumed that observations of the five pairs are independent, including those at Nest C (Table 1) where the pair was observed during consecutive nesting seasons. This assumption is likely met if the turnover rate in the study population is similar to that Newton (1982) found in a population of European Sparrow Hawks (*A. nisus*).

[1] Dept. Biol. Sci., Univ. Idaho, Moscow, Idaho 83843. (Present address of PLK: Los Alamos Technical Assoc., P.O. Box 410, Los Alamos, New Mexico 87544.)

Prey items delivered to the nests were assigned size categories of 3–27 g (Class 1), 28–91 g (Class 2), and >91 g (Class 3). These represent groups 1–3, 4–6, and 7–18 of the cubic function series of Storer (1966). Whereas most large prey could be identified to species, smaller prey delivered to the nests were often plucked or decapitated, making their identification difficult. Juvenile prey were assigned to size classes corresponding to 90% of the adult weight for the species.

Most of the prey captured by males were delivered to the nest by the females after a food transfer involving characteristic vocalizations. Prey delivered by the female without such vocalizations were assumed to have been taken by her. Our data are biased if adults consistently transport larger prey to the nest but consume some of the smaller prey, a pattern documented for other avian species (Royama 1966, Root 1967, Taylor 1979). We have no evidence that such behavior occurred during this study.

In 1978 potential avian prey were censused using a modification of the line-transect technique described by Anderson (1972). One 400-m transect was established in each of the three common habitats (Douglas fir forest, pasture, and mixed-shrub edge) near each of the monitored nest sites. Transects were censused on two consecutive mornings during the early nestling period (weeks 1–3) and the early fledgling period (weeks 4–6).

In 1979 the three habitats were sampled in proportion to their relative areas as measured from aerial photographs within a circle with a radius of 2 km around each nest, the approximate spacing distance of nesting Cooper's Hawks in Oregon (Reynolds 1975). Transects with 20 stations spaced at 60-m intervals were censused in proportion to the availability of each habitat within the defined territory. To make the data comparable to that of 1979, the 1978 indices for each habitat were multiplied by the appropriate proportion each was represented within defined territories. Frequencies within prey size classes were evaluated with respect to nesting pair (territory) and sex using log-linear analysis (Fienberg 1977).

## RESULTS

Both the sex of the bird making the capture and the size of prey taken were recorded for 224 of 286 prey delivered to the nests under observation (Table 1). Based on vocalizations or observations of the male delivering prey to the nest, we assumed that males captured 63% of these prey. Birds represented 85% of the identified prey (N = 110) (Appendix 1). American Robins (*Turdus migratorius*) and California Quail (*Callipepla californica*) comprised 52 and 47% of the identified prey captured by males and females, respectively.

The prey delivery data (Table 1) were biased because of differences in observational time between years (50% more at each nest in 1978) and in numbers of prey deliveries by the sexes (41% more by males). When the categorical data were adjusted for these biases, there was no significant difference in prey deliveries between nesting pairs ($\chi^2 = 2.0$, df = 4, $P = 0.73$), between sexes ($\chi^2 = 0.2$, df = 1, $P = 0.67$) or between prey size classes ($\chi^2 = 4.1$, df = 2, $P = 0.13$). No higher-order effects were significant.

As the abundance and proportional use of avian prey were known, we calculated electivity indices, which measure the ability (or preference) of a predator to capture a particular prey species (Lawlor 1980). These indices indicated that both males and females showed a preference for prey size

TABLE 1
NUMBER OF PREY CAPTURED BY NESTING PAIRS OF COOPER'S HAWKS, LOPEZ ISLAND, WASHINGTON

| Year | Territory | Sex | Prey size class 1 | 2 | 3 | Total |
|---|---|---|---|---|---|---|
| 1978 | A | Male | 9 (24)[a] | 19 (50) | 10 (26) | 38 |
| | | Female | 4 (24) | 9 (53) | 4 (24) | 17 |
| | C | Male | 9 (31) | 11 (38) | 9 (31) | 29 |
| | | Female | 6 (21) | 9 (31) | 14 (48) | 29 |
| 1979 | B | Male | 13 (54) | 10 (42) | 1 (4) | 24 |
| | | Female | 6 (38) | 4 (25) | 6 (38) | 16 |
| | C | Male | 8 (30) | 16 (59) | 3 (11) | 27 |
| | | Female | 6 (55) | 4 (36) | 1 (9) | 11 |
| | D | Male | 11 (46) | 9 (38) | 4 (17) | 24 |
| | | Female | 2 (22) | 3 (33) | 4 (44) | 9 |
| | | All males | 50 (35) | 65 (46) | 27 (19) | 142 |
| | | All females | 24 (29) | 29 (35) | 29 (35) | 82 |

[a] Percent of total.

Classes 2 and 3 (Table 2). Using the measures developed by Petraitis (1979), with the modification for sample size developed by Smith (1984), we found extensive overlap of the food niche between the sexes (G = 0.96; minimum 0.52; maximum 1.0), although niche breadth was moderate for both sexes (W = 0.54 for males and 0.44 for females; minimum 0; maximum 1.0).

## DISCUSSION

Of the several possible explanations for our failure to find evidence that male and female Cooper's Hawks partitioned the food resource during the nesting season, two merit discussion. As females rarely hunted during the first 3 weeks of the nestling period, food niche partitioning may have occurred only when both sexes hunted prey. There was no significant difference, however, in the prey-use patterns of males between the period when the female rarely hunted and when both sexes hunted regularly ($\chi^2$ = 1.17, df = 1, $P > 0.05$).

Another possibility is that prey-size partitioning did not occur because the population was not food stressed. Although it is difficult to make definitive statements regarding food stress, inferences can be made from an examination of food consumption rates and fledging success (Newton 1979). Under conditions of food abundance, total food consumption by raptors should increase during the nestling period and differ according to brood size. Under conditions of food scarcity, the rate of food delivery

TABLE 2
ELECTIVITY INDICES OF NESTING COOPER'S HAWKS, LOPEZ ISLAND, WASHINGTON

| Prey size class | Proportional availability | Proportional use | | Electivity index | |
|---|---|---|---|---|---|
| | | Male | Female | Male | Female |
| 1 | 0.77 | 0.36 | 0.30 | 0.47 | 0.39 |
| 2 | 0.18 | 0.46 | 0.34 | 2.56 | 1.89 |
| 3 | 0.04 | 0.19 | 0.36 | 4.75 | 9.00 |

should show little increase despite (1) the increase in demand associated with maturation or (2) differences in brood size.

Peak rates of food delivery for the 5 pairs observed during this study occurred when the nestlings were 4 weeks of age. Larger broods (4–5 young) received significantly more prey than broods with 3 young ($F = 11.0$, $P < 0.05$). The overall prey delivery rates, both in frequency (9.1 prey/nest/day), and in biomass (883 g/nest/day) exceeded those reported by Snyder and Snyder (1973) for nesting pairs of Cooper's Hawks thought to be food-limited. In addition, fledging success in this study (3.6 young/successful nest) was greater than that reported for other nesting populations of Cooper's Hawks (Craighead and Craighead 1956, Schriver 1969, Henny and Wight 1972, Reynolds 1975).

Although sex-related differences in diet have been documented for species of dimorphic raptors (Storer 1966, Schipper 1973, Opdam 1975, Snyder and Wiley 1976, Newton 1978), some nesting populations show no significant intersexual dietary differences (Schipper 1973, Balgooyen 1976, Snyder and Wiley 1976). The latter results, together with those of this study, suggest that intersexual prey-size partitioning is not a comprehensive explanation for the marked sexual size dimorphism found in many raptorial birds.

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## Appendix 1

Total Number of Identified Prey Delivered by Nesting Pairs of Cooper's Hawks, Lopez Island, Washington

| Species | No. individuals |
|---|---|
| Birds | |
| American Robin (*Turdus migratorius*) | 25 |
| California Quail (*Callipepla californica*) | 22 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 6 |
| Olive-sided Flycatcher (*Contopus borealis*) | 5 |
| Band-tailed Pigeon (*Columba fasciata*) | 4 |
| Red-breasted Nuthatch (*Sitta canadensis*) | 4 |
| European Starling (*Sturnus vulgaris*) | 4 |
| Brewer's Blackbird (*Euphagus cyanocephalus*) | 3 |
| Northern Flicker (*Colaptes auratus*) | 3 |
| White-crowned Sparrow (*Zonotrichia leucophrys*) | 3 |
| Dark-eyed Junco (*Junco hyemalis*) | 2 |
| Unidentified flycatcher (*Empidonax* sp.) | 2 |
| Northwestern Crow (*Corvus caurinus*) | 1 |
| Chestnut-backed Chickadee (*Parus rufescens*) | 1 |
| Cedar Waxwing (*Bombycilla cedrorum*) | 1 |
| Domestic chicken (*Gallus* sp.) | 1 |
| Hutton's Vireo (*Vireo huttoni*) | 1 |
| Unidentified Vireo (*Vireo* sp.) | 1 |
| Mourning Dove (*Zenaida macroura*) | 1 |
| Red-winged Blackbird (*Agelaius phoeniceus*) | 1 |
| Song Sparrow (*Melospiza melodia*) | 1 |
| Unidentified finch (*Carpodacus* sp.) | 1 |
| Mammals | |
| Townsend's Chipmunk (*Tamias townsendi*) | 9 |
| Domestic rabbit (*Oryctolagus cuniculus*) | 4 |
| Unidentified rat (*Rattus* sp.) | 2 |
| Deer Mouse (*Peromyscus maniculatus*) | 2 |

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# HUNTING SUCCESS OF SOME MISSOURI RAPTORS

BRIAN TOLAND[1]

ABSTRACT.—Hunting success varied widely among raptors studied throughout Missouri. Higher success rates occurred in raptors hunting relatively small, easily dispatched prey such as invertebrates, herpetofauna, and rodents. "Attacking" raptors, including accipiters and falcons, which concentrated hunting efforts on relatively large, agile prey (mainly birds) were significantly less successful on a per-attack basis. Young raptors were less successful hunters than were adults, and they may have compensated for relatively less developed hunting skills and flight coordination by pursing more invertebrate prey and less agile quarry than did conspecific adults. Intersexual hunting success comparisons in Northern Harriers (*Circus cyaneus*) and American Kestrels (*Falco sparverius*) indicated that males maintain slightly, but not significantly, higher capture rates than females. Females, however, captured larger prey items than their respective mates among 3 species compared (Cooper's Hawks [*Accipiter cooperii*], Northern Harriers, and Red-tailed Hawks [*Buteo jamaicensis*]). Raptors used the most successful hunting method most often, and there was a positive correlation between relative use and rate of success of each hunting strategy. *Received 27 Feb. 1984, accepted 16 Oct. 1985.*

Raptor hunting success varies with season, local weather conditions, habitat characteristics, and prey availability (Brown 1977, Newton 1979, Cade 1982). Hunting success (the percentage of all capture attempts that result in prey capture) also varies according to the age, sex, and species of raptor, as well as with the type of prey hunted. In general, juvenile and immature raptors usually exhibit lower hunting success rates than do adults, and males sometimes display higher success rates than do females (Brown and Amadon 1968, Dekker 1979, Cade 1982). Most male birds of prey are smaller than their female counterparts and they often take smaller prey (Brown 1977, Newton 1979, Cade 1982); thus males may expend less energy per capture than do females (Mosher and Matray 1974, Cade 1982). Additionally, the hunting success rates of "searching" raptors (most insect or rodent eaters) are generally higher than those of "attacking" raptors (pursuers of birds) (Fox 1977). "Searching" raptors spend most of their foraging time looking for small, numerous, relatively easy to catch animals. These raptors capture their prey from a simple, direct attack and are often successful. "Attacking" raptors prey on relatively large, less numerous, more agile animals. They spend less time searching, and their attack is often complex, energy-demanding, and sometimes prolonged (Fox 1977, Cade 1982).

Hunting success rates have been documented for several species of raptors, mostly falcons. Relatively low success rates have been reported

[1] Route 4, Box 165, Columbia, Missouri 65201.

for raptors that specialize in taking birds, including rates of 5 and 12.8% for the Merlin (*Falco columbarius*) in Europe and California, respectively (Rudebeck 1951, Page and Whitacre 1975). Rudebeck (1951) also reported a combined hunting success rate of 8% for European Sparrowhawks (*Accipiter nisus*), Peregrine Falcons (*F. peregrinus*), and Merlins. An extremely wide range of success rates (7.5–93%) for hunting peregrines has been published (Rudebeck 1951, Brown and Amadon 1968, Parker 1979, Dekker 1980, Treleaven 1980, Cade 1982).

Relatively high success rates of 89 and 82% have been documented for the fish-eating Osprey (*Pandion haliaetus*) in Europe (Brown and Amadon 1968) and North America (Ueoka and Koplin 1973). Success rates of 33–65% have been reported for the insectivorous and rodent-eating American Kestrel (*F. sparverius*), depending upon season, prey type, and geography (Jenkins 1970, Sparrowe 1972, Rudolph 1982, Collopy and Koplin 1983).

Various success rates have been reported for raptors that feed mostly upon mammals, but supplement their diets with birds and reptiles. Mader (1975) documented a rate of 16% for Harris' Hawks (*Parabuteo unicinctus*). Wakeley (1978) reported that Ferruginous Hawks (*Buteo regalis*) were successful 17% of the time in Idaho. Orde and Harrell (1977) reported a success rate of 79% for Red-tailed Hawks (*Buteo jamaicensis*) in South Dakota. Nesting Golden Eagles (*Aquila chrysaetos*) in Idaho were successful on 20% of their capture attempts (Collopy 1983). Clark (1975) calculated a success rate of about 20% for the rodent-specializing Short-eared Owl (*Asio flammeus*).

Here, I report the success rates of Missouri raptors in relation to prey hunted, sex or age of raptor, and hunting methods used.

## STUDY AREAS AND METHODS

I collected data on raptor hunting success in various habitats throughout Missouri. Field studies were concentrated in Boone, Callaway, and Cole counties; Table Rock Lake, Duck Creek Wildlife Area, Mingo and Swan Lake National Wildlife Refuges, the greater St. Louis and Kansas City areas, state park and Nature Conservancy prairies in southwest Missouri, and riparian and upland habitats in the Ozarks.

Raptors were observed through 9× binoculars or a 30× spotting scope. My observations totaled 3585 h and were divided equally by month over the 7 years of the study. To achieve equal representation throughout the day for all species, observations were made during all daylight hours, including as many full days as possible. Half-day observations were alternated between morning and afternoon. A total of 1064 h (108 days) was accumulated during full-day observations, and the remaining 2521 h were divided equally between morning and afternoon. The number of capture attempts, successful captures, and prey species taken were recorded. All capture attempts with undetermined outcomes were excluded from analysis. Prey were divided into 5 general categories (invertebrates, fish, herptiles, birds, and mammals). All raptors were identified to species. Raptors exhibiting sexual dichromatism were

sexed, including American Kestrels, Merlins, and Northern Harriers (*Circus cyaneus*). I determined age class (adult or immature) for all but Rough-legged Hawks (*B. lagopus*) which could not be aged easily at a distance or under unfavorable lighting conditions. Rough legs exhibit a considerable degree of variability in plumage patterns, further confounded by melanistic individuals which mask characteristics for aging and sexing. I identified immature American Kestrels during summer and fall using plumage characteristics described by Parkes (1955) and Roest (1957). When I was unable to confidently differentiate female and immature Northern Harriers, I placed them in the category of "unidentified brown harrier."

I also recorded the various hunting methods used by raptors including: perch-hunting (Collopy and Koplin 1983), hovering (Brown and Amadon 1968, Brown 1977, Rudolph 1982), flapping flight (quartering, coursing, tail-chasing, and contour-hugging; Brown and Amadon 1968, Brown 1977, Wakeley 1978, Cade 1982), nonflapping flight (soaring, gliding, interhover, and waiting on; Brown 1977, Grubb 1977, Cade 1982), and diving or stooping (Brown 1977, Cade 1982). I calculated the relative use of these hunting strategies by each species by timing the activities of individual birds for 20-min intervals.

## RESULTS AND DISCUSSION

Between 1 September 1978 and 31 July 1985, I observed 3266 capture attempts (58% successsful) by 17 species of raptors (Table 1). Of this total, 1512 (46.3%) of the attempts were made by American Kestrels. The four most common Missouri falconiformes (excluding Turkey Vulture, including American Kestrel, Northern Harrier, Rough-legged Hawk, Red-tailed Hawk) accounted for 2577 of 3266 (79.0%) of the hunting attempts during the 7-year period. In addition to being relatively more abundant species, these birds inhabit somewhat open habitat where they are more easily observed.

I recorded success rates ranging from a low of 18.8% for Peregrine Falcons to 69.3% for American Kestrels. Prey, which were divided into five categories, were captured with various success rates by raptors. This apparently was a function of the relative mobility of the prey and the quality of cover in the habitat. Of the five major prey categories, invertebrates (mainly insects) were most easily caught (80.0%). Reptiles and amphibians were also captured relatively easily (77.0%). Raptors had a capture rate of 57.0% when hunting small mammals (mainly mice, rats, squirrels, and rabbits). Fish were captured at a rate of 51.0%, and avian prey at a rate of 20.4%.

Of the 17 species of raptors, Northern Goshawks (*A. gentilis*) had the highest success rate in capturing birds (33%). The overall success rate (for all raptors) of 20.5% (N = 439) in capturing avian quarry is higher than rates reported by Rudebeck (1951) (7.5 and 5.0%, N = 252, 139), Page and Whitacre (1975) (12.8%, N = 343), and Parker (1979) (16%, N = 116) for Merlins and Peregrine Falcons. Some very high bird-hunting success rates, however, have been reported for Peregrine Falcons by Cade (1982) (93 and 73%, N = 102, 81) and Treleaven (1980) (62%, N = 55)

and for New Zealand Falcons (*Falco novaeseelandiae*) by Fox (1977) (55%, N = 20). Variation in success rates reported may reflect differences in local weather conditions, seasons, and prey types, or differences in sample sizes.

I compared intersexual hunting success in only two species: American Kestrels and Northern Harriers—the only raptors in Missouri that are sexually dichromatic (except for the Merlin for which the sample was too small). Male kestrels were more successful on a per-strike basis than were females, but there was no significant sex-related difference in hunting bout success ($\chi^2 = 3.46$, df = 1, $P > 0.05$). Similarly, male harriers were more successful per hunting attempt than were females, but the difference was not statistically significant ($\chi^2 = 3.17$, df = 1, $P > 0.05$) (Table 1). Higher hunting success rates of males may be an adaptation for the successful provisioning of females and young throughout most of the nesting season (Cade 1982). Females may make up for their lower rate of capture by catching larger quarry than the smaller males can. During nesting, larger prey items were consistently captured by the females of breeding pairs of Cooper's Hawks (*A. cooperii*; Toland, in press a), Northern Harriers (Toland, in press b), and Red-tailed Hawks (Toland, unpubl. data) in Missouri. By transporting larger energy packages, a female actually may be more efficient than her mate in terms of energy used per unit of energy gained (Cade 1982).

Immatures were less successful hunters than adult raptors for 8 of the 9 species (Table 1). Adult Bald Eagles (*Haliaeetus leucocephalus*) were significantly more successful per strike than were immatures ($\chi^2 = 7.14$, df = 1, $P < 0.01$). Hunting bout success in adult American Kestrels (males and females combined) was significantly greater than in immatures ($\chi^2 = 7.22$, df = 1, $P < 0.01$). Adult Red-tailed Hawks were significantly more successful per capture attempt than immatures ($\chi^2 = 7.10$, df = 1, $P < 0.01$). Swainson's Hawk (*B. swainsoni*) adults were more successful than immatures, but the small sample size precluded statistical significance. Among Broad-winged Hawks (*B. platypterus*) and Red-shouldered Hawks (*B. lineatus*) adults were more successful hunters than immatures, but the differences were not significant ($\chi^2 = 0.33$, df = 1, $P > 0.05$; $\chi^2 = 0.40$, df = 1, $P > 0.05$). Unsexed juvenile Northern Harriers were less successful per capture attempt than were either adult males or females, but the difference was not significant ($\chi^2 = 2.01$, df = 1, $P > 0.05$). Adult Cooper's Hawks were more successful than immatures, although the difference was not significant ($\chi^2 = 0.67$, df = 1, $P > 0.05$).

Immature Sharp-shinned Hawks (*A. striatus*) exhibited a higher hunting success rate than adults, but the sample was too small to test statistically. The relatively high success rates of immature Sharp-shinned Hawks, as

TABLE 1

HUNTING SUCCESS OF MISSOURI RAPTORS, 1978–85

| Species | No. successful captures/no. attempts (%) | | | | | Overall hunting success | |
|---|---|---|---|---|---|---|---|
| | Prey taken | | | | | | |
| | Invertebrates | Fish | Reptiles and amphibians | Small mammals | Birds | Total no. attempts | % |
| American Kestrel | 517/638 (81.0) | — | 8/9 (89.0) | 480/734 (65.0) | 43/133 (32.0) | 1512 | 69.3 |
| Males | 259/307 (84.4) | — | 7/8 (87.5) | 302/430 (70.0) | 32/89 (36.0) | 834 | 71.9 |
| Females | 223/272 (82.0) | — | 1/1 (100.0) | 176/294 (60.0) | 11/44 (25.0) | 610 | 67.4 |
| Immatures | 35/58 (60.0) | — | — | 2/10 (20.0) | — | 68 | 54.5 |
| Merlins (adults) | — | — | — | — | 2/8 (25.0) | 8 | 25.0 |
| Prairie Falcon (adults) | — | — | — | — | 3/14 (21.4) | 14 | 21.4 |
| Peregrine Falcon | — | — | — | — | 3/16 (18.8) | 16 | 18.8 |
| Adults | — | — | — | — | 2/8 (25.0) | 8 | 25.0 |
| Immatures | — | — | — | — | 1/8 (12.5) | 8 | 12.5 |
| Sharp-shinned Hawk | 3/4 (75.0) | — | — | — | 6/30 (20.0) | 34 | 26.5 |
| Adults | — | — | — | — | 6/24 (25.0) | 24 | 25.0 |
| Immatures | 3/4 (75.0) | — | — | — | 0/6 (0.0) | 10 | 30.0 |
| Cooper's Hawk | 3/4 (75.0) | — | 1/1 (100.0) | 11/26 (42.3) | 6/39 (15.4) | 70 | 30.0 |
| Adults | — | — | 1/1 (100.0) | 8/15 (53.3) | 6/29 (20.7) | 45 | 33.3 |
| Immatures | 3/4 (75.0) | — | — | 3/11 (27.3) | 0/10 (0.0) | 25 | 24.0 |
| Northern Goshawk (adults) | — | — | — | — | 3/9 (33.3) | 9 | 33.3 |
| Northern Harrier | 9/14 (64.3) | — | 26/35 (74.3) | 91/270 (33.7) | 13/92 (14.1) | 411 | 33.8 |
| Males | 4/5 (80.0) | — | 9/11 (81.8) | 36/88 (41.0) | 7/32 (21.9) | 136 | 41.2 |
| Females | 2/2 (100.0) | — | 9/12 (75.0) | 26/84 (31.0) | 4/33 (12.1) | 131 | 31.3 |
| Unidentified brown harriers | 2/2 (100.0) | — | 2/3 (66.7) | 17/50 (34.0) | 2/20 (10.0) | 75 | 30.7 |
| Immatures | 1/5 (20.0) | — | 6/9 (66.7) | 12/48 (25.0) | 0/7 (0.0) | 69 | 27.5 |

TABLE 1
CONTINUED

| Species | No. successful captures/no. attempts (%) | | | | | | | | | | Overall hunting success | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Prey taken | | | | | | | | | | | |
| | Invertebrates | | Fish | | Reptiles and amphibians | | Small mammals | | Birds | | Total no. attempts | % |
| Red-tailed Hawk | 44/61 | (72.0) | 2/3 | (66.7) | 18/23 | (78.3) | 212/340 | (62.4) | 6/38 | (15.8) | 465 | 60.6 |
| Adults | 10/12 | (83.3) | 2/3 | (66.7) | 17/20 | (85.0) | 131/185 | (70.8) | 6/30 | (20.0) | 250 | 66.4 |
| Immatures | 34/49 | (69.4) | — | | 1/3 | (33.3) | 81/155 | (52.3) | 0/8 | (0.0) | 215 | 54.0 |
| Red-shouldered Hawk | 11/15 | (73.3) | — | | 14/19 | (73.7) | 21/39 | (53.8) | 1/7 | (14.3) | 80 | 58.8 |
| Adults | 6/8 | (75.0) | — | | 12/16 | (75.0) | 14/24 | (58.3) | 1/6 | (16.7) | 54 | 61.0 |
| Immatures | 5/7 | (71.4) | — | | 2/3 | (66.7) | 7/15 | (46.7) | 0/1 | (0.0) | 26 | 53.8 |
| Broad-winged Hawk | 22/30 | (73.3) | — | | 9/12 | (75.0) | 16/28 | (57.1) | 0/1 | (0.0) | 71 | 66.2 |
| Adults | 12/16 | (75.0) | — | | 9/12 | (75.0) | 14/23 | (61.0) | 0/1 | (0.0) | 52 | 67.3 |
| Immatures | 10/14 | (71.4) | — | | — | | 2/5 | (40.0) | — | | 19 | 63.2 |
| Swainson's Hawk | 7/9 | (77.8) | — | | — | | 6/13 | (46.2) | — | | 22 | 59.0 |
| Adults | 2/2 | (100.0) | — | | — | | 3/6 | (50.0) | — | | 8 | 62.5 |
| Immatures | 5/7 | (71.4) | — | | — | | 3/7 | (43.0) | — | | 14 | 57.0 |
| Rough-legged Hawk | 4/5 | (80.0) | — | | — | | 101/180 | (56.0) | 0/4 | (0.0) | 189 | 55.6 |
| Osprey (adults) | — | | 71/106 | (67.0) | — | | — | | — | | 106 | 67.0 |
| Bald Eagle | — | | 41/117 | (35.0) | — | | 8/15 | (53.3) | 3/41 | (7.3) | 173 | 30.0 |
| Adults | — | | 29/60 | (48.3) | — | | — | | 2/16 | (12.5) | 76 | 40.8 |
| Immatures | — | | 12/57 | (21.0) | — | | 8/15 | (53.3) | 1/25 | (4.0) | 97 | 21.6 |
| Great Horned Owl (adults) | 2/2 | (100.0) | — | | 1/1 | (100.0) | 12/17 | (70.6) | 1/4 | (25.0) | 24 | 66.7 |
| Short-eared Owl (adults) | — | | — | | — | | 26/57 | (45.6) | 0/3 | (0.0) | 60 | 43.3 |
| All species | 622/782 | (80.0) | 115/226 | (51.0) | 77/100 | (77.0) | 984/1719 | (57.0) | 90/439 | (20.5) | 3264 | 58.0 |

well as immatures of other species, may result from immatures concentrating on smaller, more numerous, and more easily caught invertebrate prey. Excluding Bald Eagles and American Kestrels, immatures of 7 raptor species attacked invertebrates on 90 of 386 (23%) capture attempts while adults of these species pursued invertebrates only during 45 of 700 (6.4%) capture attempts. Conversely, capture of relatively large, less numerous, agile avian prey was attempted by adult raptors on 179 of 700 (25.6%) hunting bouts, but by immatures on only 41 of 386 (10.5%) attempts. Overall, immatures were successful on 237 of 551 (43%) capture attempts, in contrast to a success rate of 63% (1,404 of 2,220) for adults.

There was no significant difference in hunting success among congeneric buteos ($\chi^2 = 3.13$, df = 4, $P > 0.05$), accipiters ($\chi^2 = 0.14$, df = 2, $P > 0.05$), or the 3 larger falcons ($\chi^2 = 0.12$, df = 2, $P > 0.05$). As a group, buteos were significantly more successful hunters on a per-strike basis than either accipiters ($\chi^2 = 37.31$, df = 1, $P < 0.001$) or the larger falcons ($\chi^2 = 22.12$, df = 1, $P < 0.01$). American Kestrels were significantly more successful per capture attempt than the larger falcons ($\chi^2 = 40.55$, df = 1, $P < 0.001$). These differences were apparently due to the hunting methods used and prey types pursued by these groupings of searching and attacking raptors. There was no significant difference in hunting success between the 2 groups of attackers, namely, accipiters and larger falcons ($\chi^2 = 0.86$, df = 1, $P > 0.05$).

Of the 17 species of raptors studied, 11 were categorized as "searchers" (Fox 1977, Cade 1982). When they were combined, these 11 species accounted for 3115 of 3266 (95%) of the total hunting attempts. Searching raptors spend much of the time hunting from a relatively conspicuous perch or hover, or while systematically searching from coursing, slow, horizontal flight, and prey predominantly upon invertebrates and small mammals (Cade 1982). The hunting success of this group of raptors averaged 59%, significantly higher than the average hunting success of 27% for the "attackers," which included Northern Goshawk, Cooper's Hawk, Sharp-shinned Hawk, Peregrine Falcon, Prairie Falcon (*F. mexicanus*), and Merlin ($\chi^2 = 28.28$, df = 1, $P < 0.01$). Although they fit the searcher category, Northern Harriers were significantly less successful per attack than were buteos ($\chi^2 = 71.55$, df = 1, $P < 0.001$) and they exhibited hunting success similar to the 6 attackers ($\chi^2 = 2.05$, df = 1, $P > 0.05$). The relatively low success rate of harriers when compared to other searchers is probably a result of their atypical foraging behavior (Rice 1982). Comparative anatomical research indicates a strong convergence of the facial anatomy of harriers with that of owls (Clark and Stanley 1976). The facial ruff and associated structures, as well as the low foraging flight of both

harriers and certain owls, suggest a reliance by harriers on auditory cues when hunting (Rice 1982). Because hunting harriers often strike at prey that they probably hear but cannot see, their success may be lower than sight-hunting raptors with similar food habits. Short-eared Owls, which use similar foraging methods and habitat as Northern Harriers, had similar hunting success ($\chi^2 = 2.09$, df = 1, $P > 0.05$).

Observations of foraging raptors in these two general groupings indicated that hunting success varied according to agility of prey and size of prey relative to size of raptor. The size of prey taken by "attacking" species in Missouri averaged from 25 to 50% of the body weights of the raptors, while "searching" species took prey averaging only 5–10% of their body weights (Toland, unpubl. data). Birds (the most agile prey group) comprised 56% (23 of 41) of the successful prey captures by the 6 raptors categorized as attackers. Raptors in the searcher group captured birds on 67 of 1846 (3.6%) successful captures.

The hunting method used most frequently by each raptor was the one that resulted in the highest hunting success for each. For example, American Kestrels perch-hunted 88% of the time but only hover-hunted 10% of the time. They used flapping flight (contour-hugging and tail-chasing) and stooping only 2% of the time. Their hunting success rates for the 3 methods were 76, 52, and 45%, respectively ($\chi^2 = 79.36$, df = 2, $P < 0.001$; Toland 1983).

Buteos used perch-hunting 72%, nonflapping flight 13%, hovering 8%, and flapping flight 7% of the time. Broad-winged Hawks spent the most time perch-hunting (92%), and Rough-legged Hawks hover-hunted the most (11%). Buteos as a group were successful on nearly 60% of their capture attempts, including 71% from a perch, 50% from a hover, 25% from a glide or soar, and 18% from flapping flight.

Ospreys hunted most often from a hover (44%), followed by nonflapping flight (36%), and perch-hunting (20%). Ospreys were 75% successful when hunting from a hover, but only 55% successful when gliding or soaring, and 33% when perch-hunting. Bald Eagles used gliding and soaring, perch-hunting, and flapping flight 41, 34, and 25% of the time, respectively. Eagles were successful capturing quarry 34% of the time from nonflapping flight, 30% from a perch, and 25% from flapping flight.

Accipiters initiated 60% of their attacks from fast horizontal flapping flight (mostly contour-hugging), and hunted from a perch 40% of the time. As a group, accipiters captured their quarry 33% of the time, 35% of the time from flapping flights, and 30% of the time from a perch.

Northern Harriers hunted from a slow coursing and quartering flight more than 96% of the time. They occasionally perch-hunted from a small

tree, bush, fence post, or on the ground. Only 9 capture attempts by Northern Harriers were initiated from a perch: 33% were successful.

The 3 larger falcons used fast flapping flight (tail-chasing, coursing, and contour-hugging) and stoops during capture attempts virtually 100% of the time. As a group they had the lowest hunting success (21%).

Short-eared Owls hunted from coursing, slow flapping flight on all of the hunting bouts I observed. Conversely, Great Horned Owls initiated all of their capture attempts from a perch.

There was a positive correlation between relative use and capture success of hunting methods used by all raptor species ($r = 0.69$, $P < 0.05$). Similar results have been reported by Sparrowe (1972), Collopy and Koplin (1983), and Rudolph (1982) for American Kestrels, Shrubb (1982) for Common Kestrels (*F. tinnunculus*), and Grubb (1977) for Ospreys.

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# GENERAL NOTES

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**Growth of Shiny Cowbird and host chicks.**—The Shiny Cowbird (*Molothrus bonariensis*) is an obligate brood parasite that uses more than 180 species of birds as hosts within its range through South America and the West Indies (Friedmann et al., Smithson. Contr. Zool. 235, 1977; Manolis, Ph.D. diss., Univ. Colorado, Boulder, Colorado, 1982; Wiley, Condor 87:165–176, 1985). Although in some circumstances parasitism is advantageous to the host (Smith, Nature 219:690–694, 1968; Smith, pp. 7–15 *in* Host-parasite Interfaces, B. B. Nickol, ed., Academic Press, New York, New York, 1979), generally, cowbird parasitism has a negative effect on host reproduction by reducing productivity and nest success (reviewed in Payne, Ann. Rev. Ecol. Syst. 8:1–28, 1977). Like other forms of social parasitism (e.g., acarine nest parasites, Moss and Camin, Science 168:1000–1002, 1970; warble flies [*Philornis deceptivus*] on nestling Pearly-eyed Thrashers [*Margarops fuscatus*] and Puerto Rican Parrots [*Amazona vittata*], Arendt, Auk 102:270–280, 281–292, 1985, Wiley, pp. 137–159 *in* Conservation of New World Parrots, R. Pasquier, ed., Int. Council Bird Preserv. Tech. Bull. 1, 1980; blowflies [*Protocalliphora splendida*] on Tree Swallows [*Tachycineta bicolor*], Stahura, North Am. Bird Bander 7:140–144, 1982), avian brood parasitism may adversely affect host offspring growth and viability. Whereas Shiny Cowbird chicks do not eliminate their host nestmates by eviction or killing as do several avian parasites (reviewed in Payne 1977), the addition of the parasite chick(s) to the nest may set up competitive interactions between the species that could be detrimental to the host's offspring, particularly if the young of the host are the smaller and behaviorally less vigorous of the two species.

As part of a study of the ecology of the Shiny Cowbird and its hosts in the Caribbean, I monitored growth of cowbird and host chicks. Nestling cowbird growth rates might be suspected to vary with the size of the host species, both as a result of receiving different quantities of food concomitant with the size of the host adult, and due to competitive interactions with foster siblings of various-sized species. To test this prediction and examine growth rates in parasitized nests, I observed cowbird and host-chick growth at the nests of three species widely disparate in size: Yellow Warbler (*Dendroica petechia*), Yellow-shouldered Blackbird (*Agelaius xanthomus*), and Greater Antillean Grackle (*Quiscalus niger*).

*Study area and methods.*—I studied Shiny Cowbirds and their hosts at Roosevelt Roads Naval Station, 60 km east of San Juan, at the easternmost point of Puerto Rico. I have described the study areas in detail elsewhere (Wiley and Wiley, Wildl. Monogr. 64, 1979; Wiley 1985). Where I conducted the study, mangrove forest dominates the extensive tidal lands and accounts for about 25% (814 ha) of the station's vegetative cover. Data included here are from March through July, 1980 and 1981.

I located nests during searches through the study areas every other day. Each nest was marked with a coded tag (inconspicuously placed) and plotted on field maps. At each visit to the study areas I inspected nests to determine number of host and, if present, parasite eggs and chicks. At selected nests, chicks were weighed and measured on alternate days. Weights were taken using Pesola spring scales. Measurements were made to the nearest 0.1 mm with vernier or dial calipers and included length of exposed culmen (culmen length), length of tarsus (tarso-metatarsus), length of forearm (radius-ulna), length of seventh primary, and length of tail (Baldwin et al., Sci. Publ., Cleveland Mus. Nat. Hist. 2:1–165, 1931). Hatchlings were marked individually with food dye (blue, green, yellow, orange) on an inconspicuous part of the body (e.g., under wing). Older chicks were banded with three celluloid leg bands in unique color combinations. At some nests, I manipulated broods to

equalize chick loads among parasitized and nonparasitized pairs for more equitable growth comparisons. Chicks of equal ages were fostered into the experimental nests.

I followed statistical methods as presented by Sokal and Rohlf (Biometry, 2nd ed., Freeman, San Francisco, California, 1981), and Zar (Biostatistical Analysis, Prentice-Hall, Englewood Cliffs, New Jersey, 1975). I used a randomization approach (a Monte Carlo method) to test growth data (Sokal and Rohlf 1981:787). Randomization tests consist of three steps: (1) an observed sample of variates is considered to be one of many possible, equally probable, outcomes that could occur by chance; (2) the possible outcomes that could be obtained by randomly rearranging the variates are enumerated; and (3) from the resulting distribution of outcomes, the single observed outcome is tested with respect to whether it is improbable enough to warrant rejection of the null hypothesis; e.g., observed growth rate of a chick in a parasitized nest is not different from the rate of a chick in a nonparasitized nest. I used Sokal and Rohlf's (1981) RANTST program for computation of the randomization tests. A sample of 500 permutations of variates (#2 above) was used to obtain probability values for equivalence of mean daily growth between species or between host chicks in parasitized and nonparasitized nests. These probability values were combined (Sokal and Rohlf 1981: 779) to get an overall probability value for equivalence of mean growth of parasitized and nonparasitized nestlings or mean growth of parasite and host chicks.

*Results.*—Adult Shiny Cowbirds (male $\bar{x}$ = 38.7 ± 0.05 [SE] g, N = 479; female $\bar{x}$ = 31.9 ± 0.04 g, N = 670) averaged about 48% of adult Greater Antillean Grackle weights (male $\bar{x}$ = 86.4 ± 0.61 g, N = 89; female $\bar{x}$ = 61.7 ± 0.51 g, N = 95), 276% of adult Yellow Warbler weights (both sexes $\bar{x}$ = 12.8 ± 0.40 g, N = 12), and about the same as adult Yellow-shouldered Blackbird weights (both sexes $\bar{x}$ = 38.4 ± 1.10 g, N = 8).

Cowbird chicks had a daily mean weight of 15.1 ± 0.63 g (N = 204; this is equivalent to 0.92 blackbird chick, 0.58 grackle chick, and 1.69 warbler chick). Weighed and measured host and cowbird nestlings were from the following mean brood sizes: Yellow Warbler nests—2.7 ± 0.17 (N = 4 nests) chicks in parasitized nests, 2.0 ± 0.0 (N = 9) chicks in nonparasitized nests; Yellow-shouldered Blackbird nests, parasitized—3.8 ± 0.25 chicks (N = 4), nonparasitized—1.9 ± 0.24 chicks (N = 8); Greater Antillean Grackle nests, parasitized—1.6 ± 0.17 chicks (N =3), nonparasitized—2.9 ± 0.16 chicks (N =14). Because brood sizes between parasitized and nonparasitized hosts were not equal nor were brood sizes equivalent among the three host species, comparisons among these groups required additional interpretation. Attempts to create even brood loads among pairs by artificially manipulating brood composition and size were unsuccessful in that most of the manipulated broods failed or natural brood adjustments again altered loads.

Despite the greater brood load in parasitized nests, Yellow Warbler chicks (N = 7) sharing nests with young cowbirds showed the same absolute growth (mm or g per day) rates as chicks (N = 17) in nonparasitized nests. Grackle chicks in parasitized and nonparasitized nests also exhibited similar growth curves for weight, culmen, and tarsus. However, chicks (N = 3) at parasitized grackle nests lagged behind chicks (N = 27) at nonparasitized nests in forearm ($P = 0.05$), seventh primary ($P < 0.02$), and rectrix ($P < 0.01$) development. Yellow-shouldered Blackbird chicks (N = 8) in parasitized nests showed retarded development for weight and length of tarsus and forearm (all $P < 0.001$) compared with chicks (N = 15) at nonparasitized nests.

Absolute growth curves of cowbirds were dissimilar to those of each of the host species I studied. Yellow Warbler chicks weighed less ($P < 0.001$) and had culmen ($P < 0.001$) and forearm ($P = 0.02$) measurements that were consistently less than those of cowbird chicks of comparable ages. The tarsi of Yellow Warblers grew faster than did those of cowbird chicks ($P = 0.05$). Warbler primary feathers grew faster ($P = 0.005$) until the ninth day when feather growth of the larger cowbirds surpassed the host chicks' growth. Cowbird chicks in

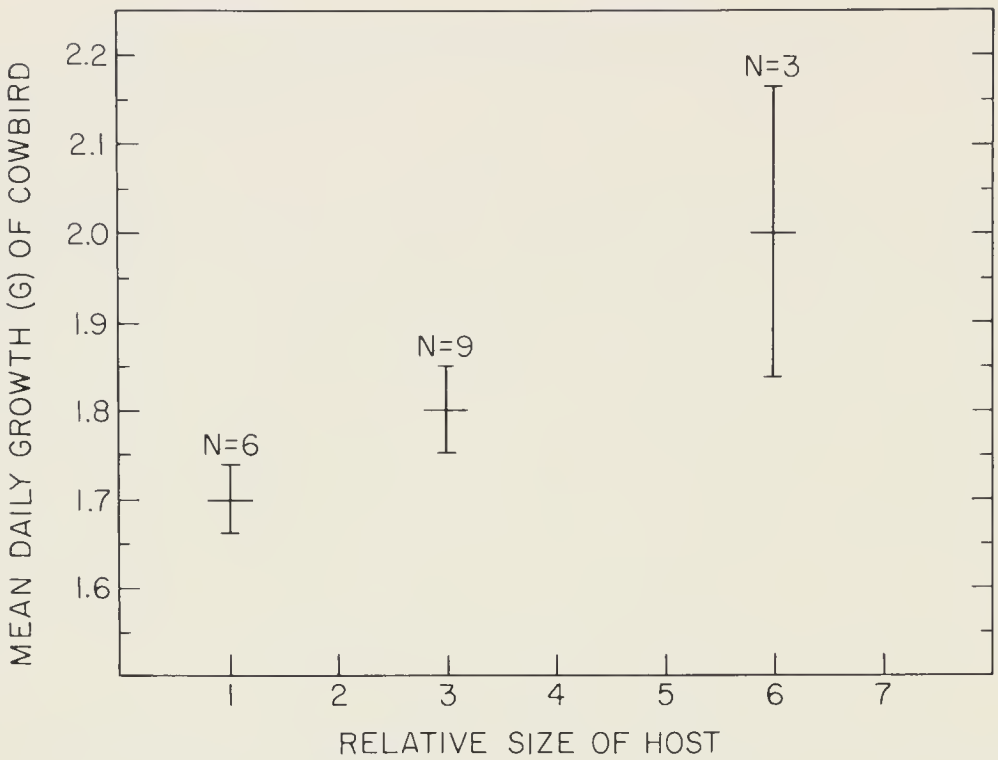


FIG. 1. Relationship of Shiny Cowbird chick growth rate (mean daily weight gain in g) to size of three host species in Puerto Rico: Yellow Warbler ($\bar{x}$ adult weight = 12.8 g), Yellow-shouldered Blackbird (38.4 g), and Greater Antillean Grackle (74.1 g). Vertical lines represent ±1 standard error.

Yellow-shouldered Blackbird nests were smaller on average than comparably aged host chicks with respect to all measurements (weight—$P < 0.02$, tarsus length—$P < 0.005$, length 7th primary—$P = 0.02$, length rectrices—$P < 0.001$), except forearm length. Grackle nestlings were heavier ($P < 0.01$) and larger (all $P < 0.001$) than equal-aged parasite chicks for all growth parameters measured.

There were also differences in relative growth rates (daily change proportionate to current size, "instantaneous daily growth"; Brody, Bioenergetics and Growth, Reinhold, New York, New York, 1945) among host and cowbird chicks. Yellow Warbler and Yellow-shouldered Blackbirds aged 0–4 days showed greater relative growth rates than Shiny Cowbird chicks ($\bar{x}$ Yellow Warbler relative growth [combined weight, and length of tarsus, culmen, forearm] = 26.5% per day; $\bar{x}$ Yellow-shouldered Blackbird = 27.3%; $\bar{x}$ Shiny Cowbird = 19.6% in both species' nests; $0.10 > P > 0.05$). The relative growth rate of Yellow Warbler chicks ($\bar{x}$ = 9.6%/day) declined to below that of Shiny Cowbird chicks ($\bar{x}$ = 10.8%/day; $P > 0.05$) from day 5 to fledging (day 10). After the host chicks had left the nest, the Shiny Cowbird chick relative growth rate continued to decline to an average of 0.7%/day. Relative growth rates of Shiny Cowbird and Yellow-shouldered Blackbird chicks were alike from days 5 to

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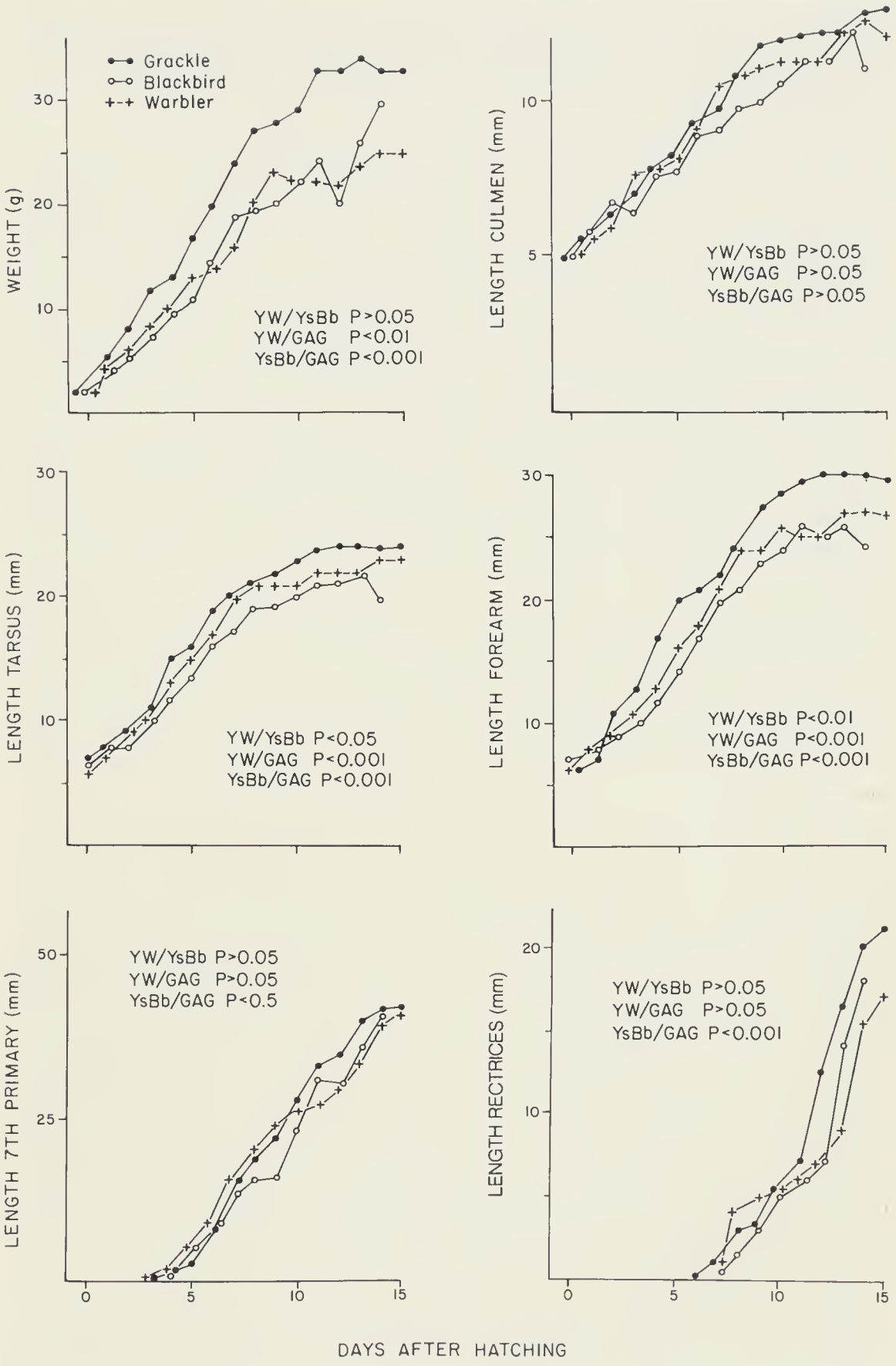
FIG. 2. Shiny Cowbird chick growth in nests of three different-sized host species (Yellow Warbler, Yellow-shouldered Blackbird, Greater Antillean Grackle) at Roosevelt Roads Naval Station, eastern Puerto Rico.


Grackle
Blackbird
Warbler
WEIGHT (g)
YW/YsBb P>0.05
YW/GAG P<0.01
YsBb/GAG P<0.001
LENGTH CULMEN (mm)
YW/YsBb P>0.05
YW/GAG P>0.05
YsBb/GAG P>0.05
LENGTH TARSUS (mm)
YW/YsBb P<0.05
YW/GAG P<0.001
YsBb/GAG P<0.001
LENGTH FOREARM (mm)
YW/YsBb P<0.01
YW/GAG P<0.001
YsBb/GAG P<0.001
LENGTH 7TH PRIMARY (mm)
YW/YsBb P>0.05
YW/GAG P>0.05
YsBb/GAG P<0.5
LENGTH RECTRICES (mm)
YW/YsBb P>0.05
YW/GAG P>0.05
YsBb/GAG P<0.001
DAYS AFTER HATCHING

10 (12.0% vs 13.4%) and days 11 through 14 (3.5% vs 2.8%; $P > 0.05$). The relative growth rates of Greater Antillean Grackle and cowbird chicks were more comparable than those of the parasite chicks and the smaller host species throughout the nestling period: days 0 to 4—grackle = 26.7%/day vs cowbird 28.3%, days 5 to 10—10.5% vs 9.4%, days 11 to 14—2.7% vs 1.3%; all $P > 0.05$.

Growth rate (absolute) of cowbirds increased significantly with host body size (product-moment correlation coefficient [$r$] = 0.996) (Fig. 1). Cowbirds raised in grackle nests showed relatively greater daily size attainment than Yellow-shouldered Blackbird-raised chicks for all growth parameters measured, except culmen length (Fig. 2). Cowbirds in grackle nests also attained greater daily weight, tarsus, and forearm growth than parasites raised in Yellow Warbler nests, although cowbird culmen and feather development were not different (Fig. 2). Despite the Yellow Warbler's smaller size, cowbirds raised by warblers showed no overall difference in weight gain or culmen and feather growth than those raised by the larger Yellow-shouldered Blackbird. However, cowbirds raised by Yellow Warblers exhibited greater tarsus and forearm growth than blackbird-raised parasites (Fig. 2).

*Discussion.*—Comparison of growth rates of host chicks at parasitized and nonparasitized nests were confounded by unevenness of brood loads among nests. Nestlings in smaller broods ($\bar{x} = 2$) of unparasitized Yellow-shouldered Blackbirds had higher growth rates than did chicks in parasitized nests where brood loads were elevated above normal (i.e., nonparasitized) brood sizes (4 vs 3 chicks). Perhaps chicks in nests with above-normal numbers of nestlings show retarded growth rates because adults are unable to supply enough food to the brood.

I found no difference in growth rates of Yellow Warbler chicks at parasitized and nonparasitized nests. Apparently, adult warblers were able to supply enough food to maintain good nestling growth for the brood sizes I studied. Chicks measured were from nonparasitized nests averaging two chicks per nest compared with parasitized nests where broods averaged an equivalent of three Yellow Warbler chicks (one warbler + one cowbird chick). Nonparasitized warblers occasionally fledge three chicks so the equivalent brood load of three nestlings may not stress adult warbler food provisioning capabilities and chicks may be expected to show growth rates comparable to two-chick nests.

Growth rates of Greater Antillean Grackle chicks in parasitized nests were retarded compared with those of chicks in unparasitized nests despite lower brood loads at the parasitized nests. The slower growth of chicks at parasitized nests may be related to the cowbird's shorter incubation period. A cowbird hatching earlier than the grackle chicks has an advantage in development, particularly begging behavior. Adults may respond to the more aggressive and better-developed begging responses of the cowbird chick by providing it with more food than the less-developed grackle nestling (Gochfeld, Living Bird 17:41–50, 1979; Wiley, Ph.D. diss., Univ. Miami, Coral Gables, Florida, 1982).

Growth rates of cowbird chicks were related to host mass. Probably this relationship was due to the amount of food supplied by the different-sized hosts (i.e., larger hosts provided chicks with greater amounts of food than smaller hosts). I did not attempt to determine whether various host species were supplying different quantities of foods to chicks, although casual observations made from blinds at nests suggested this was true. However, this apparent relationship could have been partly an effect of different brood loads in the nests of the three host species I studied; i.e., parasitized warbler and blackbird nests held greater equivalent chick loads than did grackle nests (three and four vs fewer than two at grackle nests).

Parasitized blackbird nests carried relatively larger brood loads than parasitized Yellow Warbler nests, which may have contributed to the lower growth rates of cowbirds raised by blackbird- compared to warbler-raised parasites. Also, sample size was small for older blackbird-raised cowbirds, which may have contributed to the oscillation in weights during the last few days in the nests.

Presumably, chicks fledging at heavier weights are more likely to survive than lighter fledglings as they have energy reserves to see them through the critical period of early flight and independence from their foster parents. If the relationship between host size and cowbird chick growth rate is real, one would expect parasites to choose nests of larger species (or individuals) in which to deposit their eggs. There are several possible disadvantages, however, to parasitizing large species, including: (1) birds larger than the cowbird could inflict serious injury to the parasite if the latter is caught at the nest, (2) large birds normally lay larger eggs and hatchability of parasite eggs is lower in nests with large host eggs than in nests of hosts similar in size to the cowbird (Wiley 1982), and (3) competitive interactions between large host chicks and cowbird chicks (particularly where host brood sizes are normal; all the parasitized grackle nests I watched had below average brood sizes) may put the parasite nestlings at a disadvantage in obtaining food from the adult. Therefore, I would expect cowbirds to parasitize species larger than grackles only rarely.

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**Autumn Sandhill Crane habitat use in southeast Oregon.**—Greater Sandhill Cranes (*Grus canadensis tabida*) of the Central Valley Population (CVP) are residents of the Pacific states and southern British Columbia, nesting primarily in southcentral and eastern Oregon and northeast California (Littlefield and Thompson, Proc. Int. Crane Workshop 2:113–120, 1979). Although the population has been studied extensively since the mid-1960s, many aspects of the life history of the population have not been presented.

Considerable information has been published on roosting habitat (e.g., Lewis, Proc. Int. Crane Workshop 1:93–104, 1976; Bennett, M.S. thesis, Univ. Wisconsin, Stevens Point, Wisconsin, 1978; Lovvorn and Kirkpatrick, J. Wildl. Manage. 45:842–857, 1981) and field use (Guthery, M.S. thesis, Texas A&M Univ., College Station, Texas, 1972; Lovvorn and Kirkpatrick, J. Wildl. Manage. 46:99–108, 1982) of Sandhill Cranes in the west central and midwestern states. Most studies, however, were on wintering and traditional spring and autumn stopover areas, and little information has been published on an autumn staging area. Melvin and Temple (Proc. Int. Crane Workshop 3:73–87, 1981) defined an autumn staging area as a locality where cranes congregate during the first segment of fall migration, usually no more than a day's flight from nesting areas, whereas a traditional stopover area was described as a congregation area along the migration route. Malheur National Wildlife Refuge (NWR), Harney Co., in southeast Oregon has been the major fall staging area for the CVP at least since the late 1930s.

TABLE 1
YEAR AND PEAK NUMBER OF GREATER SANDHILL CRANES ON MALHEUR NATIONAL WILDLIFE REFUGE, OREGON

| Year | N | Year | N |
|---|---|---|---|
| 1938 | 700 | 1962 | 1350 |
| 1940 | 766 | 1963 | 1740 |
| 1941 | 700 | 1964 | 1500 |
| 1942 | 989 | 1965 | 1800 |
| 1943 | 1165 | 1966 | 2000 |
| 1944 | 1500 | 1967 | 2400 |
| 1945 | 1500 | 1968 | 2000 |
| 1946 | 1000 | 1969 | 2000 |
| 1947 | 1200 | 1970 | 2929[a] |
| 1948 | 1000 | 1971 | 2711 |
| 1949 | 800 | 1972 | 974 |
| 1950 | 1000 | 1973 | 1319 |
| 1951 | 1000 | 1974 | 563 |
| 1952 | 1000 | 1975 | 2056 |
| 1953 | 1000 | 1976 | 1651 |
| 1954 | 500 | 1977 | 2855 |
| 1955 | 2000 | 1978 | 2614 |
| 1956 | 2000 | 1979 | 3408 |
| 1957 | 1400 | 1980 | 2157 |
| 1958 | 2000 | 1981 | 2179 |
| 1959 | 2000 | 1982 | 2502 |
| 1960 | 1200 | 1983 | 2295 |
| 1961 | 1200 | 1984 | 2720 |

[a] Since 1970, cranes have been counted individually.

As with other populations of Sandhill Cranes, the CVP declined after European settlement (Littlefield and Thompson 1979). From the 1930s through the 1960s, however, the subspecies increased in numbers in the Pacific states. The population reached a peak in 1970, then began declining in portions of its nesting range. Concern for the CVP was first reported in the mid-1970s as low annual recruitment became evident after 1972 (Littlefield, Proc. Int. Crane Workshop 1:86–92, 1976). In 1982, the population was placed on the U.S. Fish and Wildlife Service Sensitive Species List for Region 1, and in 1983 was classified as rare on the California State List.

In autumn, grainfields and favorable roosting sites attract cranes onto Malheur NWR before birds migrate southwest to wintering areas in the California Central Valley. Autumn Sandhill Crane numbers were estimated from 1938 through 1969; however, counts of individuals begun in 1970 have continued through 1984 (Table 1). Information on roost sites and autumn crane use collected from 1966 through 1984 is summarized in this report.

*Study area.*—Malheur NWR, Oregon, contains 73,219 ha, is 43 km at its widest point, and is 77 km long. The majority of habitat within the refuge consists of shallow marsh-native meadows with an interspersion of shrub-grass covered uplands. Approximately 325 ha of grainfields provide autumn feeding habitat for Sandhill Cranes. All grainfields are located within 7.6 km of roosting sites.

*History of autumn crane use.*—Successful grain farming occurred on Malheur NWR between 1940 and the mid-1960s. The farming program was limited from the mid-1960s until 1975. During this period, there was no grain production in some years, resulting in limited autumn crane use. Since 1975, grain crops have been present annually. During poor crop years, peak crane numbers were low, but with consistent grain production after 1975, numbers increased (Table 1). Information on autumn use before 1938 was not available.

Formerly, while cranes were moving onto Malheur NWR in late September and early October, other cranes, which had been present since July and August, began leaving for wintering areas. As grain farming stabilized after 1975, this early departure has been mostly eliminated. However, in some years, inclement weather conditions have resulted in earlier than normal departure.

*Autumn staging.*—Sandhill cranes usually start to move onto refuge grainfields in mid-July. However, in some years, a few cranes visit fields in late June, these birds probably being unsuccessful pairs that had nested locally. In drought years, a larger number of cranes concentrated on the refuge in July as food sources elsewhere within the summer range of the population became depleted. This condition occurred in 1973 and 1977 when 393 and 238 cranes, respectively, were recorded between 15–31 July (Table 2).

Crane numbers were relatively stable through August, with the major influx not occurring until late September and early October. Peak numbers were usually present by mid-October, but if mild fall weather persisted or an abundance of feeding areas was available off the refuge, the peak was delayed until early November.

Fall migration usually began in October. In 1969 and 1971, however, cereal grain production was minimal, and the last cranes were observed in 1969 on 24 September (30) and in 1971 on 9 September (1). Cranes were seen leaving the refuge on 23 August 1968, another year with low food availability (E. McLaury, pers. comm.). Normally, the majority of cranes migrated between 1–15 November. In 1981, no cranes were seen after 1 November although an abundance of food was available. The 1981–82 winter in southeast Oregon was one of the most severe in recent years and this probably contributed to their early departure. Occasionally, a few cranes lingered into December, but normally all had migrated by the end of November (Table 3). Latest fall departures were recorded on 10 December 1947 (2), 20 December 1951 (1), 31 December 1961 (1), 11 December 1965 (1), and 15 December 1977 (4). The mean departure date for 39 years was 16 November.

Based on color-marked birds, unsuccessful nesting pairs and subadults were usually the first to arrive on refuge grainfields, and these individuals were often the first to migrate. Pairs with young were among the last to migrate. This behavior was similar to that reported from other Sandhill Crane concentration areas (Herter, Proc. Int. Crane Workshop 3:273–280, 1981; Miller and Hatfield, J. Wildl. Manage. 38:234–242, 1973).

*Roosting sites.*—Several roosting sites on Malheur NWR have been used regularly since studies began in 1966. These sites included Buena Vista Pond, Diamond Pond, and Boca Lake. Mean water depth at roosting sites was 11.7 cm (range = 4.0–22.4 cm). Water depths at Malheur NWR were within the range of those reported elsewhere (Lewis 1976; Lovvorn and Kirkpatrick 1981; Perkins and Brown, Arizona Game and Fish Dept. Spec. Publ. 11, 1981). All refuge sites were in types 3, 4, and 10 wetlands as described by Shaw and Fredine (U.S. Fish and Wildl. Serv. Circ. 39, 1971). Roost sites averaged 2.2 km (range = 0.8–7.6 km) from feeding areas. Distances from roost sites to grainfields were less than those reported for Sandhill Cranes on wintering and traditional stopover areas (Lewis 1976; Crete and Toepfer, U.S. Fish and Wildl. Serv. Rept., Twin Cities, Minn., 1978; Lovvorn and Kirkpatrick 1982). Distances flown to feeding sites did not seem influenced by weather conditions as reported from other regions (Guthery 1972; Lovvorn and Kirkpatrick 1982; Perkins and Brown 1981; Walkinshaw, The Sandhill Cranes, Cranbrook Inst. Sci. Bull. 29, Bloomfield

TABLE 2

NUMBER OF GREATER SANDHILL CRANES ON THE MALHEUR NWR STAGING AREA

| Period | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 15 Jul.–31 Jul. | 393 | 160 | — | 148 | 238 | 61 | — | — | — | 25 | — | 133 |
| 1 Aug.–15 Aug. | 452 | 309 | 276 | 188 | 317 | 176 | 251 | 248 | 335 | 324 | 120 | 242 |
| 16 Aug.–29 Aug. | 545 | 421 | 328 | 215 | 453 | 205 | 359 | 348 | 398 | 338 | 206 | 257 |
| 30 Aug.–12 Sept. | 664 | 580 | 448 | 441 | 698 | 284 | 402 | 425 | 524 | 377 | 413 | 418 |
| 13 Sept.–26 Sept. | 795 | 580 | 860 | 617 | 1160 | 795 | 709 | 1028 | 771 | 583 | 1049 | 943 |
| 27 Sept.–10 Oct. | 201 | 111 | 957 | 1637 | 2623 | 2016 | 2663 | 1631 | 1525 | 2340 | 2295 | 1921 |
| 11 Oct.–24 Oct. | 45 | — | 1565 | 1145 | 2855 | 2614 | 2016 | 2157 | 2179 | 2346 | 537 | 2720 |
| 25 Oct.–14 Nov. | — | — | 2279 | 395 | 2067 | 849 | 3408 | 647 | 422 | 2502 | 4 | 82 |
| 15 Nov.–28 Nov. | — | — | 597 | — | 1039 | — | 6 | 404 | — | 179 | — | 5 |
| 29 Nov.–15 Dec. | — | — | — | — | 57 | — | 2 | — | — | 1 | — | — |

TABLE 3

LATEST FALL OBSERVATIONS OF GREATER SANDHILL CRANES AT MALHEUR NWR, OREGON

| Year | Date | N | Year | Date | N |
|---|---|---|---|---|---|
| 1944 | 19 Nov. | (150) | 1966 | 17 Nov. | (2) |
| 1945 | 17 Nov. | (76) | 1967 | 6 Dec. | (13) |
| 1946 | 13 Nov. | (3) | 1968 | 23 Nov. | (23) |
| 1947 | 10 Dec. | (2) | 1969 | 24 Sept. | (30) |
| 1948 | 8 Nov. | (2) | 1970 | 1 Dec. | (6) |
| 1949 | 4 Nov. | (3) | 1971 | 9 Sept. | (1) |
| 1950 | 11 Nov. | (5) | 1972 | 7 Nov. | (65) |
| 1951 | 20 Dec. | (1) | 1973 | 18 Nov. | (1) |
| 1952 | 20 Nov. | (10) | 1974 | 23 Oct. | (?) |
| 1955 | 2 Nov. | (12) | 1975 | 23 Nov. | (13) |
| 1956 | 3 Nov. | (300) | 1976 | 11 Nov. | (75) |
| 1957 | 22 Nov. | (1) | 1977 | 15 Dec. | (4) |
| 1958 | 20 Oct. | (10) | 1978 | 3 Nov. | (49) |
| 1959 | 15 Oct. | (50) | 1979 | 5 Dec. | (2) |
| 1960 | 14 Oct. | (130) | 1980 | 31 Dec. | (2)[a] |
| 1961 | 31 Dec. | (1) | 1981 | 31 Oct. | (368) |
| 1962 | 14 Nov. | (13) | 1982 | 31 Dec. | (1)[a] |
| 1963 | 30 Nov. | (10)) | 1983 | 7 Nov. | (4) |
| 1964 | 17 Nov. | (100) | 1984 | 16 Nov. | (5) |
| 1965 | 11 Dec. | (1) | | | |

[a] Wintered.

Hills, Michigan, 1949). The close proximity of Malheur NWR grainfields to roost sites probably accounted for this difference.

Sandhill Crane intolerance to human disturbance seemed less important on Malheur NWR than reported elsewhere (Lewis 1976, Perkins and Brown 1981). The Diamond Pond Roost was within 100 m of a well-traveled highway and was bordered on one side by a dike and three sides by low growth saltgrass (*Distichlis stricta*). Saltgrass separated the site from the highway. Buena Vista Roost was within 0.8 km of a human residence, but visibility was restricted by dense hardstem bulrush (*Scirpus acutus*). Other roost sites on the refuge, however, were isolated from human activity.

Roost sites on Malheur NWR have ranged from ca 0.5 to 120 ha. As with other reported roost sites, water was clear with little turbidity. Lewis (1976) reported winter roost sites had little submergent vegetation, whereas Bennett (1978) and Lovvorn and Kirkpatrick (1981) found cranes used sites with heavy submergent growth in Wisconsin and Indiana, respectively. Roost sites had no substantial growths of submergent vegetation on Malheur NWR.

*Loafing sites.*—The nearest water from feeding areas was often used for loafing, but some cranes regularly flew to the roost site used the previous night. Loafing sites included shallow ponds, sloughs, lakes, and canals. Loafing areas other than roosting sites were usually small bodies of water with short vegetation. Visibility was sometimes restricted along canals, but usually a few cranes stood on adjoining uplands while other birds loafed in the canal. Dry areas near loafing sites were often used for sitting and sleeping. Dominant vegetation on loafing sites included giant burreed (*Sparganium eurycarpum*), foxtail barley (*Hordeum jubatum*), creeping wildrye (*Elymus triticoides*), and saltgrass. Mowed, flooded meadows were used extensively when available.

*Feeding sites.*—Most autumn feeding sites on Malheur NWR were in barley fields; however, in some years oat, rye, and wheat fields also were used. Refuge crop plantings have been entirely of barley in recent years. Cranes showed no special preference among oats, rye, and barley, but did prefer wheat when it was available. Wheat has also been reported as a preferred autumn food from other areas within the species' range (Bennett 1978, Hoffman, Proc. Int. Crane Workshop 1:35–43, 1976; Munro, J. Wildl. Manage. 14:276–284, 1950; Stephen, Can. Wildl. Serv. Rept. 2, 1967).

Fields used for feeding ranged from 10 to 138 ha. Cranes periodically shifted feeding sites and preferred harvested areas. Shortly after passage of harvesting equipment, cranes moved onto the stubble. Three factors were believed responsible for this behavior: (1) An abundance of loose grain: before harvest, cranes pluck an entire seed head and pick each kernel from the head individually. This behavior was not necessary after harvest, as seeds were readily available on the ground. (2) Increased visibility: coyotes (*Canis latrans*) commonly hunt in grainfields in the fall; no cranes have been observed being attacked by coyotes in unharvested fields, but some losses may occur. Coyotes were observed attacking and killing adult cranes on four occasions in 1979. These attacks were in harvested areas, but dense vegetation adjacent to irrigation ditches provided the necessary concealment for surprise attacks. Unharvested grain probably provides additional concealment habitat for mammalian predators. (3) Increased escape capabilities: Sandhill Cranes usually escape by running until take-off speed is attained. In tall vegetation, cranes have been seen returning to the ground after their initial leap because of insufficient speed for flight. Golden Eagles (*Aquila chrysaetos*) regularly hunted over crane feeding areas. Cranes left fields rapidly when eagles approached, and take-off capabilities were improved with the shorter vegetation in harvested fields.

*Discussion.*—Malheur NWR has a long history of use in autumn by Sandhill Cranes. Cereal grain crops have been available during most years since the 1930s. These crops provide a valuable food source for premigratory cranes in the Pacific Flyway. Compared to other Sandhill Crane populations (Drewien, Ph.D. diss., Univ. Idaho, Moscow, Idaho, 1973; Crete and Toepfer 1978; Melvin and Temple 1981), the CVP has a relatively short distance (ca 465 km) to migrate before reaching its wintering areas. Unlike other populations, however, the CVP has to migrate against prevailing southwest winds. Few days in autumn have favorable migratory conditions in southeast Oregon. Favorable conditions normally last 3–4 days; therefore, it is perhaps important for cranes to have sufficient energy reserves to make the flight. Although some CVP members do stop between Malheur NWR and the California Central Valley, others have been known to fly nonstop.

The importance of protected and abundant autumn food sources may have been underestimated. If Malheur NWR grainfields were eliminated, the majority of the CVP possibly could be detrimentally affected (ca 80–85% congregate on Malheur NWR in autumn). This would be so particularly if alternate feeding areas were not available within the population's summer and fall range. In addition, with continual degradation of California wintering habitat, it may become essential to attract and maintain cranes in southeast Oregon for longer periods.

In the Great Lakes states, Crete and Toepfer (1978), Melvin and Temple (1981), and Walkinshaw and Hoffman (Jack-Pine Warbler 52:102–114, 1974) reported the rapid departure of Sandhill Cranes on the opening day of waterfowl hunting. I have seen similar behavior in southeast Oregon. Protected feeding and roosting sites (nonhunted) on Malheur NWR have provided ideal autumn habitat for the CVP for the past 40 years. Presently, the refuge is probably the most important autumn use area for Greater Sandhill Cranes in the Pacific states.

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**Diets of House Sparrows in urban and rural habitats.**—The House Sparrow (*Passer domesticus*) is a familiar and important member of the urban avifauna. A close association with man has been a major factor in its success (Summers-Smith, The House Sparrow, Collins, London, England, 1967; Robbins, pp. 3–9 *in* A Symposium on the House Sparrow [*Passer domesticus*] and European Tree Sparrow [*P. montanus*] in North America, S. C. Kendeigh, ed., Ornithol. Monogr. 14, 1973). Despite its abundance and widespread distribution, relatively little is known of the ecology and behavior of the House Sparrow in urban habitats. Previous studies of food habits (Kalmbach, U.S. Dept. Agric. Tech. Bull. 711, 1940; Southern, Annals Appl. Biol. 32:57–67, 1945; Hammer, Danish Rev. Game Biol. 1: 3–59, 1948) generally have focused on agricultural populations. More recently, Seel (Ibis 111:36–47, 1969) reported diets of nestlings from suburban areas and agricultural villages in England.

The objectives of this study were to determine the food habits of urban House Sparrows during the breeding season, and to compare their diet with that of nearby rural sparrows. We also tested the reliability of tartar emetic (antimony potassium tartrate) as a technique for collecting food samples from sparrows.

*Study area and methods.*—The study area comprised separate urban and rural areas in Centre County, Pennsylvania. A 1.3-km$^2$ portion of the Borough of State College constituted the urban site, and included the business district plus neighboring residential areas. The urban area was arbitrarily divided into 15 blocks of approximately equal area, each containing one sparrow trap site. The rural area consisted of nine farms 8–16 km from State College. All were small family farms, 60–80 ha in size, raising dairy or beef cattle and crops primarily of corn and hay.

House Sparrows were captured in mist nets or unbaited Potter traps from 26 April through 28 July 1981 and were classified by age and sex. A trapping schedule of 2 days in the urban area to 1 day in the rural area was established to maintain fairly equal numbers of captures in each habitat throughout the study period. Also, a rotation of farms and urban trap sites was followed to ensure equal trapping pressure over the study areas. All trapping was done between 06:00 and 15:00 EDT.

Two methods were employed to obtain food samples from captured House Sparrows: (1) tartar emetic (antimony potassium tartrate), a local stomach irritant, was administered to all birds to stimulate regurgitation; and (2) a sample of sparrows was sacrificed and their stomachs removed. Each bird received an oral 0.4-cc dose of 0.5% solution of tartar emetic, and was placed in a darkened box lined with a plastic tray for 15 min. Regurgitated food was rinsed from the tray into storage vials containing 10% formalin solution. After treatment with the emetic, 322 birds were sacrificed. Stomachs and crops were removed and preserved in 10% formalin.

In the laboratory, food samples were rinsed on a nylon net sieve of 28 meshes/cm, and volumes of regurgitated and combined stomach and crop samples (hereafter called stomach samples) were measured by water displacement. Food items were identified with the aid of

TABLE 1

FREQUENCY OF OCCURRENCE (PERCENT) OF FOOD CATEGORIES AND FOOD ITEMS IN THE DIETS OF URBAN AND RURAL HOUSE SPARROWS IN CENTRE COUNTY, PENNSYLVANIA, 26 APR.–28 JUL. 1981

| Food category or item | Urban (N = 218) | | Rural (N = 267) | |
|---|---|---|---|---|
| Commercial cereal grains | 66.5[a] | (19.3)[b] | 97.3 | (73.0) |
| Corn (*Zea mays*) | 42.7 | (6.9) | 86.1 | (49.4) |
| Oats (*Avena sativa*) | 0.0 | (0.0) | 8.9 | (4.1) |
| Wheat (*Triticum aestivum*) | 5.0 | (3.2) | 7.8 | (3.7) |
| Unidentified grains | 40.8 | (11.5) | 60.3 | (15.7) |
| Commercial birdseed | 61.9 | (25.7) | 2.9 | (0.7) |
| Millet (*Panicum miliaceum*) | 35.8 | (9.6) | 1.8 | (0.3) |
| Milo (*Sorghum vulgare)* | 49.5 | (14.7) | 2.9 | (0.3) |
| Sunflower (*Helianthus annuus*) | 7.3 | (1.4) | 0.3 | (0.0) |
| Other seeds | 81.2 | (21.6) | 47.9 | (1.8) |
| Grass and weed seeds | 45.9 | (3.2) | 32.2 | (1.8) |
| Compositae | 2.8 | (0.5) | 1.4 | (0.3) |
| *Oxalis* spp. | 17.9 | (0.0) | 3.4 | (0.0) |
| *Panicum* spp. | 0.0 | (0.0) | 0.3 | (0.0) |
| *Polygonum* spp. | 18.8 | (1.8) | 12.4 | (0.0) |
| *Setaria* spp. | 8.7 | (0.0) | 1.4 | (0.3) |
| *Stellaria* spp. | 10.6 | (0.5) | 16.8 | (1.1) |
| Unidentified grass seed | 9.6 | (0.0) | 3.7 | (0.0) |
| Unidentified seeds | 25.7 | (0.9) | 21.7 | (0.0) |
| Elm mast (*Ulmus americana*) | 56.4 | (18.3) | 2.2 | (0.0) |
| Plant fragments | 47.2 | (2.7) | 62.9 | (2.2) |
| Anthers | 5.9 | (0.0) | 8.9 | (0.3) |
| Flower parts | 3.2 | (0.4) | 2.6 | (0.0) |
| Grass fragments | 26.1 | (0.4) | 46.1 | (0.0) |
| Leaf fragments | 19.7 | (1.3) | 17.6 | (1.4) |
| Unidentified plant fragments | 8.7 | (0.4) | 4.1 | (0.3) |
| Insects and arachnids | 93.1 | (10.5) | 94.3 | (6.7) |
| Coleoptera | 79.8 | (6.4) | 82.0 | (5.6) |
| Carabidae | 0.0 | (0.0) | 1.1 | (0.3) |
| Curculionidae | 3.6 | (0.0) | 4.4 | (0.3) |
| Unidentified Scarabidae | 0.0 | (0.0) | 1.4 | (0.3) |
| Japanese beetle (*Popillia japonica*) | 30.2 | (3.6) | 20.2 | (1.8) |
| Unidentified Coleoptera | 55.0 | (2.7) | 64.4 | (2.6) |
| Insect larvae and pupae | 26.6 | (3.2) | 26.2 | (1.1) |
| Gypsy moth (*Lymantria dispar*) | 4.1 | (0.9) | 0.3 | (0.0) |
| Unidentified larvae | 22.4 | (2.2) | 24.7 | (1.1) |
| Unidentified pupae | 0.9 | (0.0) | 2.9 | (0.0) |
| Other insects | 49.5 | (0.9) | 41.2 | (0.0) |
| Collembola | 3.6 | (0.0) | 1.4 | (0.0) |
| Diptera | 1.3 | (0.0) | 1.1 | (0.0) |

TABLE 1
CONTINUED

| Food category or item | Urban (N = 218) | | Rural (N = 267) | |
|---|---|---|---|---|
| Hemiptera | 0.9 | (0.0) | 0.0 | (0.0) |
| Unidentified Homoptera | 2.7 | (0.0) | 4.4 | (0.0) |
| Aphididae | 4.1 | (0.0) | 3.7 | (0.0) |
| Unidentified Hymenoptera | 3.2 | (0.0) | 2.2 | (0.0) |
| Formicidae | 4.1 | (0.4) | 1.8 | (0.0) |
| Orthoptera | 0.0 | (0.0) | 1.1 | (0.0) |
| Insect eggs | 1.8 | (0.0) | 0.7 | (0.0) |
| Unidentified insects | 37.1 | (0.4) | 34.8 | (0.0) |
| Arachnida | 0.9 | (0.0) | 0.3 | (0.0) |
| Miscellaneous items | | | | |
| Parasites | 30.2 | (0.0) | 26.5 | (0.3) |
| Acarina | 29.3 | (0.0) | 25.8 | (0.0) |
| Cestoda | 6.8 | (0.0) | 4.1 | (0.3) |
| Mallophaga | 0.4 | (0.0) | 0.3 | (0.0) |
| Siphonaptera | 0.4 | (0.0) | 0.7 | (0.0) |
| Bread | 5.0 | (2.2) | 0.3 | (0.0) |

[a] Includes all samples (regurgitated, stomach) obtained from a bird.
[b] Numbers in parentheses are the percentage of times the food category or item was the volumetrically most important item in a regurgitated sample.

a reference collection and seed and insect keys, and were ranked visually in order of volume. The efficiency of the emetic was evaluated by comparing the volume and composition of regurgitated samples with the birds' total stomach contents.

Food items in each sample were combined for statistical analysis into five categories: commercial cereal grains, commercial birdseed, other seeds, plant fragments, and insects and arachnids. To ensure that no food items present in a bird were missed, only combined stomach and regurgitated samples from sacrificed birds were used. Loglinear analysis (Bishop et al., Discrete Multivariate Analysis: Theory and Practice, MIT Press, Cambridge, Massachusetts, 1975) was used to determine differences in food habits of urban and rural House Sparrows. The method uses a contingency table to detect interactions among variables under the null hypothesis of independence. Each contingency table included habitat (urban or rural), sex, age (juvenile or adult), and presence or absence of a food category. To examine significant interactions in more detail, log-odds of presence versus absence of a food category were calculated for each sex and age class in each habitat. Standard errors and approximate 95% simultaneous confidence intervals were calculated according to Haberman (Analysis of Qualitative Data, Vol. 1, Academic Press, New York, New York, 1978).

*Analysis of diets.*—Food samples were collected from 218 urban and 267 rural House Sparrows; 322 of these birds (158 urban, 164 rural) were sacrificed to obtain stomach contents after being treated with tartar emetic. Commercial cereal grains (97.3% of samples) and insects (94.3%), primarily coleopterans, were the most frequently occurring foods of rural House Sparrows (Table 1). Insects (93.1%), other seeds (81.2%), cereal grains (66.5%), and commercial birdseed (61.9%) were important foods of urban birds. Birdseed in urban birds and cereal grains in rural birds were the most important food categories by volume in regurgitated samples.

TABLE 2

LOGLINEAR MODELS AND GOODNESS-OF-FIT STATISTICS FOR PRESENCE OR ABSENCE OF FOOD CATEGORIES IN HOUSE SPARROWS

| Food category | Model[a] | df | $G^2$ | $P^b$ |
|---|---|---|---|---|
| Commercial cereal grains | Y = FH + AH + AS + E | 8 | 13.06 | 0.109 |
| Commercial birdseed | Y = FH + AS + FA + E | 8 | 4.86 | 0.772 |
| Other seeds | Y = FH + AH + AS + E | 8 | 11.45 | 0.177 |
| Plant fragments | Y = FH + AH + AS + E | 8 | 9.84 | 0.276 |
| Insects and arachnids | Y = AH + AS + F + E | 9 | 9.00 | 0.437 |

[a] Y = ln(expected cell count), F = presence or absence of food category, H = habitat, A = age, S = sex, E = error term.
[b] Nonsignificant ($P > 0.05$) test statistic indicates good model fit.

The simplest loglinear model predicting the presence or absence of cereal grains in House Sparrows included interactions between grains and habitat, age and habitat, and age and sex ($P < 0.05$) (Table 2). The only significant difference in consumption of grains was between urban and rural juvenile males (Table 3). All rural birds, however, were more likely than urban birds to consume grain, and adults were more likely to do so than juveniles.

The presence of commercial birdseed in House Sparrows was affected by interactions between birdseed and habitat, age and sex, and birdseed and age ($P < 0.05$) (Table 2). Among adult sparrows, urban birds consumed birdseed significantly more often than rural birds (Table 3). All categories of urban sparrows ate more birdseed than rural birds did, and urban adults ate more than juveniles.

The simplest model describing the presence of other seeds in House Sparrows included interactions between seeds and habitat, age and habitat, and age and sex ($P < 0.05$) (Table 2). Urban birds consumed other seeds more frequently than did rural sparrows, with juvenile males being most likely to include other seeds in their diets ($P < 0.05$) (Table 3). Significant differences also existed between rural adult males and urban adults, and between rural adult females and urban adult males.

The model describing the occurrence of plant fragments in House Sparrows included interactions between plant fragments and habitat, age and habitat, and age and sex ($P < 0.05$) (Table 2). No differences were detected in log-odds ($P > 0.05$) (Table 3); however, rural birds were generally more likely to eat plant fragments than were urban birds.

Consumption of insects and arachnids by sparrows was influenced by interactions between age and habitat, and between age and sex ($P < 0.05$) (Table 2). There was no significant effect of habitat on presence of this food category in sparrows. There were also no differences in log-odds of the presence of insects and arachnids in different groups of sparrows ($P > 0.05$) (Table 3). However, urban birds, except for juvenile males, were somewhat more likely to consume insects and arachnids than were rural birds.

*Efficiency of the emetic.*—Of 485 birds treated with tartar emetic, 93% regurgitated food. The 322 sparrows that were sacrificed following treatment with the emetic regurgitated an average of 58.3% (range 0–100%) of the total volume of food in the stomach and crop. Food remained in the crops of only 9.3% of those sparrows.

Not all food in a sparrow was regurgitated; therefore, it was necessary to determine if the regurgitated sample was representative of the composition of the total stomach contents in a bird. To do this, the number of food categories present in a bird was compared with the number of categories in the regurgitated sample. Twenty-seven percent (N = 322) of the birds were missing one or more categories in the regurgitated sample.

TABLE 3

LOG-ODDS[a] OF THE PRESENCE OF FOOD CATEGORIES IN HOUSE SPARROW STOMACHS

| Food category | Habitat | Age | Sex | Log-odds ± SE | 95% confidence interval[b] |
|---|---|---|---|---|---|
| Commercial cereal grains | Urban | Adult | Female | 0.759 ± 0.282 | −0.014, 1.532 |
| | | | Male | 1.141 ± 0.292 | 0.341, 1.940 |
| | | Juvenile | Female | 2.120 ± 0.864 | −0.247, 4.490 |
| | | | Male | −0.232 ± 0.395 | −1.310, 0.848 |
| | Rural | Adult | Female | 4.533 ± 1.420 | 0.643, 8.420 |
| | | | Male | 4.533 ± 1.420 | 0.643, 8.420 |
| | | Juvenile | Female | 3.664 ± 1.432 | −0.256, 7.580 |
| | | | Male | 3.555 ± 0.828 | 1.290, 5.830 |
| Commercial birdseed | Urban | Adult | Female | 0.456 ± 0.269 | −0.281, 1.193 |
| | | | Male | 0.681 ± 0.265 | −0.045, 1.407 |
| | | Juvenile | Female | −0.143 ± 0.536 | −1.610, 1.330 |
| | | | Male | −0.903 ± 0.433 | −2.090, 0.287 |
| | Rural | Adult | Female | −4.533 ± 1.420 | −8.420, −0.643 |
| | | | Male | −3.412 ± 0.830 | −5.680, −1.142 |
| | | Juvenile | Female | −3.662 ± 1.432 | −7.580, 0.256 |
| | | | Male | −4.673 ± 1.420 | −8.560, −0.783 |
| Other seeds | Urban | Adult | Female | 1.630 ± 0.355 | 0.660, 2.600 |
| | | | Male | 1.876 ± 0.368 | 0.866, 2.880 |
| | | Juvenile | Female | 1.526 ± 0.698 | −0.384, 3.440 |
| | | | Male | 3.932 ± 1.428 | 0.022, 7.840 |
| | Rural | Adult | Female | 0.000 ± 0.292 | −0.800, 0.800 |
| | | | Male | −0.522 ± 0.302 | −1.350, 0.308 |
| | | Juvenile | Female | 0.731 ± 0.477 | −0.579, 2.040 |
| | | | Male | 0.037 ± 0.272 | −0.713, 0.787 |
| Plant fragments | Urban | Adult | Female | 0.313 ± 0.267 | −0.419, 1.045 |
| | | | Male | −0.220 ± 0.252 | −0.910, 0.470 |
| | | Juvenile | Female | −0.747 ± 0.572 | −2.320, 0.823 |
| | | | Male | 0.077 ± 0.393 | −1.000, 1.160 |
| | Rural | Adult | Female | 0.522 ± 0.302 | −0.305, 1.350 |
| | | | Male | 0.171 ± 0.293 | −0.629, 0.974 |
| | | Juvenile | Female | 0.511 ± 0.462 | −0.759, 1.780 |
| | | | Male | 1.099 ± 0.314 | 0.239, 1.960 |
| Insects and arachnids | Urban | Adult | Female | 3.100 ± 0.647 | 1.330, 4.870 |
| | | | Male | 3.730 ± 0.826 | 1.470, 5.990 |
| | | Juvenile | Female | 3.296 ± 1.440 | −0.654, 7.250 |
| | | | Male | 1.861 ± 0.575 | 0.281, 3.440 |
| | Rural | Adult | Female | 2.520 ± 0.556 | 0.750, 4.290 |
| | | | Male | 2.520 ± 0.556 | 1.000, 4.040 |
| | | Juvenile | Female | 2.512 ± 0.849 | 0.182, 4.840 |
| | | | Male | 4.673 ± 1.421 | 0.783, 8.560 |

[a] Within a food category, a higher log-odds indicates increased likelihood of consumption of the food by that group of birds; no comparisons were made across food categories.

[b] Simultaneous confidence intervals are shown for each habitat-age-sex category of birds; categories may have been combined in certain comparisons.

TABLE 4

FREQUENCIES OF OCCURRENCE OF FOOD CATEGORIES IN REGURGITATED AND STOMACH SAMPLES FROM HOUSE SPARROWS (N = 322) IN CENTRE COUNTY, PENNSYLVANIA, 29 MAY–28 JUL. 1981[a]

| Food category | Regurgitated | Stomach[b] |
|---|---|---|
| Commercial cereal grains | 246 | 274 |
| Commercial birdseed | 77 | 91 |
| Other seeds | 189 | 220 |
| Plant fragments | 148 | 185 |
| Insects and arachnids | 286 | 310 |

[a] Frequencies of food categories in regurgitated and stomach samples were not different ($\chi^2 = 2.29$, df = 4, $P > 0.05$).
[b] Includes stomach and regurgitated samples combined for each bird.

Although use of tartar emetic causes food categories present in individual birds to be missed, the technique still gives a reliable indication of the diet of a population as long as certain foods are not consistently overlooked. For the 322 sacrificed House Sparrows, the frequencies of food categories in regurgitated samples were not different from those present in the birds ($P > 0.05$) (Table 4).

*Discussion.*—Food items were tabulated by frequency of occurrence, and statistical analysis was based on presence or absence of a food category in a bird. Problems exist with all methods of food analysis (Hartley, Ibis 90:361–381, 1948). Frequencies have the disadvantage that food items may receive the same rating whether a small fragment or a full crop is present. A combination of frequencies and volumes of items may be most useful (Korschgen, pp. 233–251 *in* Wildlife Management Techniques, R. H. Giles, Jr., ed., The Wildlife Society, Washington, D.C., 1971), but volumes were too small to measure in House Sparrows. Instead, major items were ranked visually by volume in each sample.

Urban and rural House Sparrows differed significantly in their use of food categories, probably reflecting differences in food availability to these opportunistic feeders (Kalmbach 1940). Urban sparrows relied on more food sources than did rural sparrows. Rural birds consumed primarily cereal grains and insects, mostly coleopterans. In urban sparrows, on the other hand, grains, birdseed, other seeds (primarily mast), and insects (primarily coleopterans) were all important foods. Urban sparrows may not have a single food source as abundant and consistently available as grains are for rural sparrows.

Corn was the most important cereal grain in the diet of rural House Sparrows. In our study area, feed corn was grown and stored on most farms. Sparrows presumably obtained corn from fields, waste feed, and animal dung.

Corn was present in fewer than half of the urban birds. Here, corn and other grains probably were derived from commercial birdseed mixtures. Bird feeding is common in State College, even during summer. Geis (U.S. Fish and Wildl. Serv., Spec. Sci. Rep. Wildl. 233, 1980) found that coarsely cracked corn in feeders was eaten by several species of birds, including House Sparrows, but he considered wheat and oats to be relatively unattractive.

The commercial birdseed category included only sunflower, millet, and milo; it was consumed by 61.9% of urban birds and was most often ranked number 1 in regurgitated samples. If we had grouped corn, wheat, and oats with commercial birdseed for urban House Sparrows, birdseed would have been recorded in 82.6% (180/218) of urban samples. Insects

and arachnids were more frequent (93.1%), but birdseed was much more important volumetrically.

Birdseed in urban birds and commercial cereal grains in rural birds were consumed more frequently by adult sparrows than by juveniles. Juveniles and nestlings are known to consume more animal matter and fewer seeds than adults (Kalmbach 1940). No age differences, however, were noted in the use of other seeds, which were often smaller and softer than birdseed or grains. Age differences in the use of some food items may have been blurred as older juveniles acquired adult food habits.

Coleopterans were the most important insect foods of both urban and rural House Sparrows. Resistance of the tough exoskeleton to digestion may bias results in favor of beetles over softer bodied insects. House Sparrows, however, are likely to encounter many beetles as they forage along the ground.

The significant difference between habitats in consumption of other seeds was largely due to the preponderance of elm seeds in urban birds. The Borough of State College has many elms as street trees, and sparrows exploited elm mast as a food source.

House Sparrows probably ingested plant fragments inadvertently while feeding on seeds and insects. Plant fragments rarely were the most abundant food category in a sample. Approximately twice as many rural as urban birds consumed grass fragments. This was due to the inclusion of hay and straw among the grass fragments. Rural sparrows probably ingested such fragments while foraging for waste grain in manure and barnyards.

House sparrows often were observed feeding on discarded food and refuse, especially in the urban area. The extent of this feeding was difficult to determine, as much of this food may have been digested too quickly to be detected in food samples.

Examination of regurgitated and residual stomach samples from a large number of birds showed that tartar emetic gave a reliable representation of the frequency of occurrence of food categories in the sparrow population, even though food items in individual birds often were missed. The emetic was also relatively quick and easy to administer and took effect rapidly. This minimized the amount of time between catching a bird and obtaining a food sample, reducing the possibility that easily digested food items could not be identified. Sparrows were sacrificed or released approximately 15 min after treatment with the emetic. All birds appeared healthy when released, but subsequent mortality was not determined. Zach and Falls (Can. J. Zool. 54:1599–1603, 1976) used tartar emetic on captive Ovenbirds (*Seiurus aurocapillus*), and most birds regurgitated; however, 12.5–50.0% died within a week.

*Conclusions.*—The bulk of the food consumed by both urban and rural House Sparrows came directly or indirectly from man. Management of House Sparrows through control of these food sources should therefore be feasible, although difficult as sparrows will readily exploit alternate food sources. Furthermore, the major spring and summer food of urban sparrows in our study area, commercial birdseed, cannot be made less available without affecting other species that frequent bird feeders and reducing the enjoyment of many urban residents.

Diets of House Sparrows were affected by age and sex of the birds as well as by habitat. Probable reasons include maturation of juveniles and differences in foraging behavior or dominance in relation to the dispersion pattern of different food types. Among urban birds, higher use of birdseed by adults may have been due in part to their dominance over young birds at food patches (feeders). When they fed on other seeds, a similar but more widely dispersed food source, juveniles consumed as much or more than adults.

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**Vegetation structure and Vesper Sparrow territory location.**—Vegetation structure can affect avian habitat selection (e.g., Whitmore, Wilson Bull. 91:592–598, 1979; Meents et al., Auk 98:818–827). As it also affects reproductive success in some species (Wray and Whitmore, Auk 96:802–805, 1979; Redmond et al., Can. J. Zool. 60:670–675, 1982), it should therefore affect territory location. Wray and Whitmore (1979) found that Vesper Sparrow (*Pooecetes gramineus*) reproductive success was positively correlated with percent litter cover and vertical vegetation density, and negatively correlated with percent bare ground around the nest. I tested the hypothesis that vegetation structure also affects where Vesper Sparrows locate their territories.

The study site was located on an upland grassy ridge in central west Montana, 1.4 km north of Missoula, Missoula County (114°W, 47°48′N; elevation 980 m). The vegetation was mostly mixed grasses and forbs of variable height and density.

In the first three weeks of April 1983, I established four plots, each of which was a 175 ×

Table 1

Mean Values (Standard Deviation) of Continuous Variables Used in the Discrimination of Grid Points from Used and Unused Areas

| Variable | Used (N = 52) | Unused (N = 88) |
|---|---|---|
| Vegetation height (cm) | | |
| Mean at the grid point | 20.23 (13.1) | 22.67 (18.5) |
| Mean at 1 m | 24.01 (10.9) | 31.26 (18.5) |
| Mean at 5 m | 28.97 (9.5) | 34.47 (10.8) |
| % ground cover[a] | 351.26 (29.1) | 343.25 (36.7) |
| % grass cover[a] | 144.96 (94.9) | 125.82 (76.8) |
| % forb cover[a] | 206.30 (95.6) | 217.96 (76.7) |
| Vertical vegetation density[b] | 3.54 (1.8) | 3.49 (1.9) |
| Horizontal vegetation density[c] | | |
| At 1 m | 505.63 (275.7) | 633.27 (333.7) |
| At 5 m | 1710.45 (758.2) | 2163.85 (984.5) |
| Height of nearest perch (cm) | 90.00 (39.0) | 93.7 (24.0) |
| Distance from grid point to nearest perch (m) | 9.32 (6.4) | 8.06 (5.5) |

[a] Cumulative percent cover (max = 400).
[b] Mean number of contacts with vegetation.
[c] Cumulative percent cover (max = 4000).

TABLE 2

THE STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS FOR THE STEP-WISE DISCRIMINANT FUNCTION ANALYSIS (DFA) BETWEEN "USED" AND "UNUSED" HABITAT, AND FOR THE DIRECT DFA BETWEEN "USED" AND RANDOM GRID POINTS

| Variable | Used vs unused | Used vs random |
|---|---|---|
| Vegetation height (1 m) | 0.64 | 0.63 |
| Vertical vegetation density | −0.24 | −0.15 |
| % ground cover | −0.77 | −0.93 |
| Horizontal vegetation density | 0.70 | 0.66 |

125-m grid made up of 7 × 5 sample points spaced at 25-m intervals (average territory size on my study area in 1982 was 1.65 ha, N = 60). Grids were set up within a 3-week period. I assumed that early vegetation structure was important in determining territory location and that the vegetation structure changed minimally during the early nesting period. Grids were established along a previously marked census route that included territories of Vesper Sparrows during the previous year and that showed activity early in the study. Territories were mapped using the flush method (Wiens, Ornithol. Monogr. 8, 1969). Flight paths that overlapped a neighbor's territory were excluded. Territories were considered nonoverlapping, abutting at a boundary determined by observing interactions between neighbors. Fifty-two grid points occurred in six territories and were considered to represent "used" areas; 88 grid points occurred outside territories and were considered to represent "unused" areas. Plots within a territory were not considered to differ with regards to data analysis, so that an unused area within a territory was still considered "used."

To compare territory and nonterritory vegetation, I set up four, 5-m transects at each grid point. The transects followed each of the four cardinal directions. Vegetation variables included (1) Percent cover of grass, forb, and ground; (2) Vegetation height at the grid point, and at 1 and 5 m from the grid point along the transect; (3) Vertical vegetation density, determined by lowering a thin rod vertically through the vegetation at the grid point and counting the number of contacts with vegetation (Wray and Whitmore 1979); (4) Horizontal vegetation density, determined by using a 40 × 100-cm board painted in a checkerboard of 0.1 $m^2$ that was placed narrow end down at 1 and 5 m from the grid point. The percent of each square covered by vegetation was estimated and then summed for total board cover. These measurements were made with the observer at the grid point looking from 75 cm above the ground (to simulate the view from a Vesper Sparrow perch); (5) The height of the nearest structure I considered a potential perch, and its distance to the grid point. This was determined subjectively, based on relative heights of a given structure and the surrounding vegetation. Measurements along the four transects were summed to make a composite value for each variable at each grid point.

Vegetation structure data at grid points in used and unused areas (Table 1) were compared using step-wise discriminant function analysis (DFA). To test the significance of the DFA results I used the linear function in a classification analysis, where grid-point-variable values for each grid point are entered in the linear equation, and then each point is classified as "used" or "unused" based on which group mean each was nearest. The classification results were then compared with an "expected" value based on chance sorting of grid points. Chance sorting into two categories results in 50% correct classification, and this was tested using a $\chi^2$ test. Used and unused grid points were also compared with 52 randomly selected grid points.

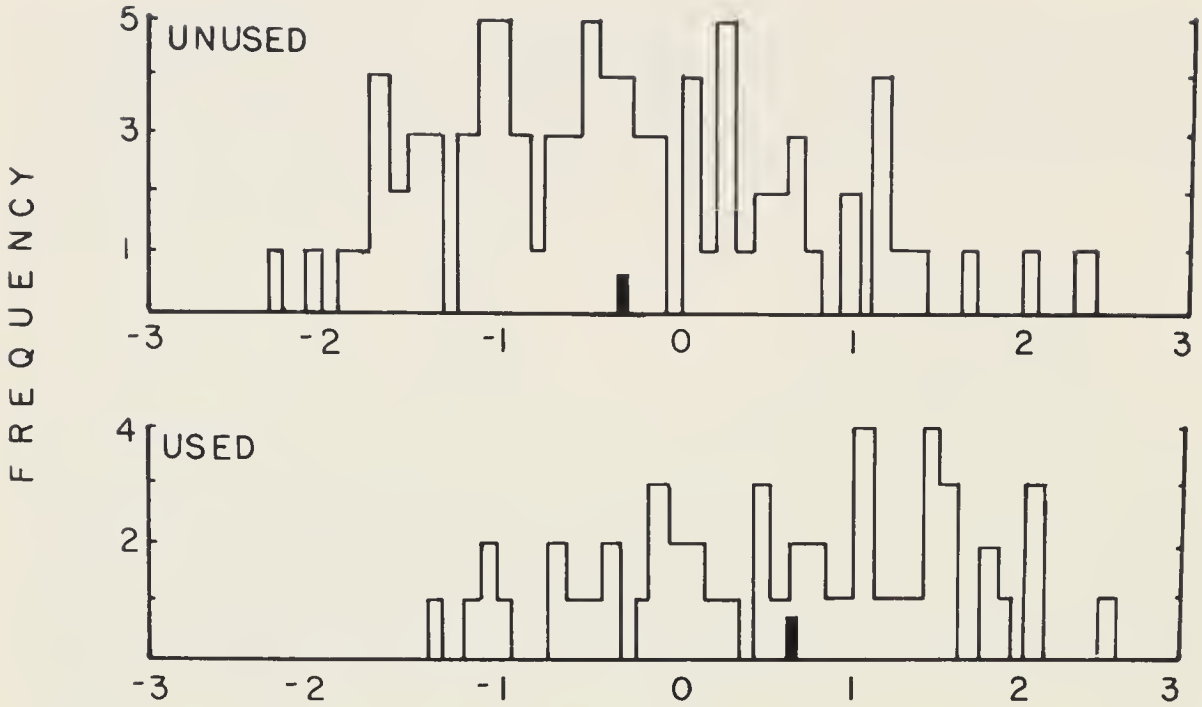


FIG. 1. Canonical discrimination function axis showing the distribution of grid points from used and unused areas. The continuum can be interpreted as going from short, dense vegetation with a high percent of ground cover (+3) to patchy tall vegetation (−3). Group means are marked with a thick vertical bar.

Maximum discrimination of vegetation structure between used and unused grid points was attained with four variables (Wilks' Lambda = 0.82, $P < 0.001$): vegetation height at 1 m, horizontal vegetation density at 1 m, percent bare ground, and vertical vegetation density (standardized canonical description function coefficients (SCDFC) are in Table 2). The distribution of points from unused to used areas along the discriminant function axis (Fig. 1) can be interpreted as a continuum from tall, patchy vegetation in unused areas (−3, group mean = −0.359), to short, dense vegetation with a relatively high percent ground cover in used areas (+3, group mean = 0.608). The height of vegetation 1 m from the grid point and horizontal vegetation density 1 m from the grid point varied inversely with percent bare ground and vertical vegetation density.

In classification analysis, 69% of the 140 grid points were classified correctly, significantly more than the 50% expected by chance sorting ($\chi^2 = 20.2$, df = 1, $P < 0.005$).

Using the four significant variables in the first DFA, grid points in used areas were successfully discriminated from random points using direct DFA (Wilks' Lambda = 0.89, $P < 0.02$) (Table 2), and more points were classified correctly (61%) than expected by chance sorting ($\chi^2 = 7.23$, df = 1, $P < 0.025$). Analysis did not discriminate between the vegetation structure of unused and random grid points (Wilks' Lambda = 0.93, $P > 0.10$), and no more grid points were classified correctly (54%) than expected by chance sorting ($\chi^2 = 0.90$, df = 1, $P > 0.05$).

A possible explanation for discrimination success between points in used and unused areas is that adjacent grid points may be more similar than nonadjacent points. Discrimination would then be an artifact of sampling. To look at variability between adjacent and nonadjacent points, I chose two sets of 36 grid points. One set was chosen at random from the four grids, and the second set consisted of the middle-most point and the eight surrounding points in each of the four grids. These represented random and clumped points

TABLE 3

STANDARD DEVIATIONS OF THE FOUR VARIABLES IMPORTANT IN THE DISCRIMINANT FUNCTION ANALYSIS (VALUES ARE FROM 36 RANSOM GRID POINTS AND 36 CLUMPED POINTS WITHIN FOUR GRIDS)

| | | Grid number | | | |
|---|---|---|---|---|---|
| | Random | 1 | 2 | 3 | 4 |
| Vegetation height (1 m) | 11.2 | 8.0 | 9.9 | 12.8 | 10.7 |
| Vertical vegetation density | 2.2 | 1.2 | 0.7 | 1.5 | 2.0 |
| % ground cover | 28.4 | 29.7 | 16.5 | 46.8 | 29.0 |
| Horizontal vegetation density | 318.4 | 93.8 | 145.8 | 462.2 | 325.6 |

respectively. The variability of each of the four variables important in discrimination was similar (Table 3).

Vesper Sparrows were found in areas where the vegetation was short and dense, with a relatively high percentage of ground cover, and not in areas where the vegetation was tall and patchy. In this study vegetation structure in used areas was similar to that found in territories of Vesper Sparrows with high reproductive success as described by Wray and Whitmore (1979). Wray and Whitmore (1979) stated that the higher amount of ground cover may be needed to conceal nests from predators. During the breeding season Vesper Sparrows feed primarily on arthropods (Evans, Am. Midl. Nat. 72:57–75, 1964), and it may be easier for birds to forage in short dense vegetation. Although my results are consistent with previous research, they are based on a small sample size, and caution should be used in generalizing from them.

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**Male and female parental care in Tree Swallows.**—Often, it is assumed that to maximize their fitness, parental investment by males in raising altricial nestlings is substantial in monogamous species (e.g., Trivers, pp. 136–197 *in* Sexual Selection and the Descent of Man, 1871–1971, E. C. Campbell, ed., Aldine Press, Chicago, Illinois, 1972; Emlen and Oring, Science 197:215–233, 1977; Wittenberger, pp. 271–349 *in* Handbook of Behavioral Neurobiology, Vol. 3, Social Behavior and Communication, P. Marler and J. G. Vandenbergh, eds., Plenum Press, New York, New York, 1979). Although some Tree Swallows (*Tachycineta bicolor*) mate polygynously (Quinney, Auk 100:750–754, 1983), most are monogamous. They are relatively short-lived and almost exclusively single-brooded (but see Hussell, Wilson Bull. 95:470–471, 1983). Plumage characteristics distinguish first year females from males and other females, but the plumage of older birds is monomorphic. Nestlings are brooded by their mothers until they are about 5 days old (Dunn, Wilson Bull. 91:455–457, 1979), they are fed aerial insects, and the fecal sacs produced by the young are

removed from the nest cavities. Thus, if typical assumptions are correct, male assistance in these activities should entail a contribution comparable to that of females. Here, I report the proportion of food deliveries, size of meals delivered and nest sanitation activity by male and female Tree Swallows mated monogamously.

*Methods.*—I studied a population of Tree Swallows breeding in nestboxes at the Port Rowan, Ontario (42°37′N, 80°27′W) secondary waste treatment ponds (hereafter, Sewage Lagoon). Nesting Tree Swallows have occupied Sewage Lagoon since 1977 when nestboxes were first erected. Plywood nestboxes stood about 1.5 m above ground attached to metal poles. All poles were fitted with large, metal cone-shaped collars that excluded terrestrial predators. Nestboxes were either 5 or 24 m apart, and were placed around the perimeter of the two ponds. Most of the 40–66 boxes have been occupied (minimum of one egg laid) every year, since 1977.

Nestboxes were visited three times daily to determine hatching times. A mean hatch date was calculated for each brood and ninth primary feathers were measured when members of a brood averaged 16 days old. Nestlings fledged at about 20 days but will leave their nests prematurely if handled after they are 16 days old. During the nestling period, adults were trapped in their nestboxes, sexed by the presence of a brood patch or cloacal protuberance, banded with U.S. Fish and Wildlife Service bands if not previously banded, and color-marked individually with magic marker on the throat, abdomen, and under-tail coverts. I did not collect data from first-year females because very few of them nested, and one-year-old females appear to differ from older ones in several reproductive variables (De Steven, Ibis 120:516–523, 1978). Most observations were made with an 8 mm movie camera that took single frame exposures each time a bird entered and left a nestbox. Observers with binoculars or telescopes watched additional boxes. Tree Swallows captured flying insects and delivered numerous items to their young in boluses of food. We trapped some adults inside their nestboxes and collected samples of food boluses before they were fed to the nestlings to determine meal sizes. I assumed that a meal was delivered each time a parent entered its nestbox.

*Results.*—We observed 10 pairs of swallows for 335 h in June 1984. During this period, 6590 meals were delivered to nestlings, of which 51% were provided by males (Table 1). On average, each brood received a meal every 3 min during daylight h (nestlings were not fed at night). Male and female deliveries did not vary greatly when nestlings were 5–10 days old (males: 49–55%, females: 45–51%). Generally, males removed fecal sacs more frequently than females, but there was more variation in fecal sac removal than in feeding (Table 1). Males and females delivered meals to their young that were similar in size (about 28 mg dry, N = 12 males and 12 females). This was close to the mean value of 24 mg (N = 48) observed in other years (Quinney, unpubl. data).

When a mate died, the remaining parent successfully raised nestlings alone. Two females and one male died during handling when their nestlings were between 4 and 9 days old. Sixteen of the 17 nestlings raised by a single parent fledged, but the remaining nestling that had been raised by a male died at 24 days. Nestlings in a brood of three young raised by a female grew as well as those raised by both parents in broods of the same size (Table 2) and better than broods of three raised by two parents in a population 3.25 km distant (Backus Field) where food was much less abundant than at Sewage Lagoon (Quinney and Ankney, Auk 102:245–250, 1985). The female that raised three young delivered an average of 234 meals daily to her brood during the week when the nestlings were 6–12 days old. Broods of three of the same age raised by both parents at Sewage Lagoon received an average of 272 meals daily. Nestlings in larger broods raised by a single parent did not grow as rapidly as those raised by two parents at either location (Table 2). There were no 7-nestling broods at Backus Field, where all of the nestlings died (presumably from starvation) in two broods of smaller size (Table 2). No broods failed completely at Sewage Lagoon.

TABLE 1

FOOD DELIVERIES AND FECAL SAC REMOVAL BY MALE AND FEMALE TREE SWALLOWS

| Nestbox | Brood size | Brood age (days) | Hours observed | Number of food deliveries (%) | | | Number of fecal sacs removed (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Male | Female | Total | Male | Female | Total |
| 5 | 6 | 6–12 | 90 | 1223 (51) | 1169 (49) | 2392 | 264 (58) | 189 (42) | 453 |
| 20 | 6 | 2–3 | 34 | 223 (53) | 199 (47) | 422 | | | |
| 39 | 6 | 5–7 | 31 | 435 (58) | 315 (42) | 750 | 89 (77) | 26 (23) | 115 |
| 44A[a] | 4 | 4–12 | 118 | 877 (47) | 995 (53) | 1872 | 149 (60) | 97 (40) | 246 |
| 45 | 4 | 6–9 | 52 | 572 (54) | 490 (46) | 1062 | 69 (38) | 114 (62) | 183 |
| 6A,[b] 34B, 43, 44, 52 | 4–7 | 2–14 | 10 | 41 (45) | 51 (55) | 92 | | | |
| All | 4–7 | 2–14 | 335 | 3371 (51) | 3219 (49) | 6590 | 571 (57) | 426 (43) | 997 |

[a] Earlier, this male fathered a brood in a box nearby. Data presented here were collected after the nestlings in his first brood had fledged.
[b] Data from these 5 nestboxes are combined because each was observed only briefly.

TABLE 2
LENGTH OF NINTH PRIMARY (MM) OF 16-DAY-OLD TREE SWALLOWS

| Location | Nestlings raised by | Brood size 3 | 6 | 7 |
|---|---|---|---|---|
| Sewage Lagoon | male and female | 51.2 (3)[a] | 49.2 (15) | 48.8 (6) |
| | female only | 52.3 (1) | | 40.7 (1) |
| | male only | | | 35.3 (1) |
| Backus Field | male and female | 45.1 (7)[b] | 49.0 (4)[b] | |

[a] (Number of broods.)
[b] Excludes measurements from one brood where all nestlings died, apparently from starvation.

Delivery rates indicate that, on average, broods of 6 young, 4–16 days old raised by both parents, received about 2300 mg wet weight of insects per h. Weatherhead (Condor 86:187–191, 1984) estimated that the mean maximum weight of a fecal sac voided by a nestling 4–16 days old was about 390 mg. Therefore, parents at Sewage Lagoon removed about 1300 mg of fecal sacs hourly, or about 57% of the wet weight of insects delivered to their young.

*Discussion.*—Broods of six young received an average of about 250 meals per day through the 20-day nestling period. Each parent provided meals of the same size and in equal proportions to their nestlings. The equitable allocation of food provisioning duties by the sexes is consistent with the hypothesis that male assistance in brood-rearing is substantial in monogamous species raising altricial offspring. I cannot explain why males generally removed a disproportionate number of fecal sacs (57%) or why the number of fecal sacs removed by each sex was more variable than the number of food deliveries. Perhaps age and experience are important in this regard. Sample sizes were small, but my results indicate that although both parents were not required to raise nestling Tree Swallows when food was abundant (see also Gowaty, Am. Nat. 121:149–157, 1983), the growth of nestlings in large broods raised by single parents was inferior to that of nestlings raised by both parents (see also Weatherhead, Auk 96:391–401, 1979). Furthermore, I do not know whether the survival of single parents was affected by their increased workload. Emancipation of male Tree Swallows would facilitate polygynous matings. An important test would compare the behavior of assisted and unassisted females, and the growth and survival of their nestlings in both marginal and good food habitats.

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**Extrapair copulations in the Tree Swallow.**—Observations of extrapair copulations and male mate guarding are varied in the Hirundinidae. Beecher and Beecher (Science 205: 1282–1285, 1979) reported that male Bank Swallows (*Riparia riparia*) guarded their mates

closely during the female's fertile period. Similar observations were recorded by Samuel (Ohio J. Sci. 71:125–128, 1971) and Woods (Abstract presented at 100th annual meeting of the American Ornithologists' Union, Chicago, Illinois, 1982) on Barn Swallows (*Hirundo rustica*). Emlen (Auk 71:16–35, 1954) observed forced copulation attempts of female Cliff Swallows (*H. pyrrhonota*) and Butler (Auk 99:758–761, 1982) suggested that wing fluttering by Cliff Swallows collecting mud was a means by which females avoid extrapair copulations. He did not observe mate guarding. Both mate guarding and extrapair copulations are well known in Purple Martins (*Progne subis*) (Allen and Nice, Am. Midl. Nat. 47:606–665, 1957; Brown, Auk 95:588–590, 1978; Morton, Abstract presented at 102nd annual meeting of the American Ornithologists' Union, Lawrence, Kansas, 1984). Leffelaar and Robertson (Behav. Ecol. Sociobiol. 16:73–79, 1984) did not observe extrapair copulations in the Tree Swallow (*Tachycineta bicolor*) and demonstrated that males do not guard their mates.

In this note I report two dissimilar cases of extrapair copulations observed during a 4-year study (1980 to 1983) of Tree Swallow social behavior. The study site was a salt marsh on the south shore of Long Island, New York (for a description of the area see Schaeffer, East. Bird Band. Assoc. News 34:216–222, 1972).

On 28 May 1982, I observed a pair of Tree Swallows that had completed egg laying on 23 May. I had previously observed a female in full iridescent blue-green plumage making several trips to the box to incubate. Only females incubate in this species. Observations began at 09:55. At the start of the observation period, the male was perched on the nest-box pole, and the female was in the nest-box hole looking out. At 10:07 a female in immature, brown plumage (Cohen, J. Colo.-Wyo. Acad. Sci. 12:44, 1980; Hussell, J. Field Ornithol. 54:312–318, 1983) approached the nest box. The male left his perch immediately and attacked the brown female as his mate watched from the nest-box hole. The male aggressively chased the brown female for a short distance, and she flew from view. The male returned to his perch on the nest-box pole. Less than one min after the chase, the resident female left the box and flew from view. After the resident female departed, a brown female approached the box (it is unknown whether she was the same brown female observed earlier) and landed on the top of the nest box. Almost immediately, the male copulated with the brown female. The brown female then flew from view, and the male returned to the top of the nest box. The blue-green female returned and was seen incubating later that day. Because no nonresident females were ever captured incubating (N = 78 breeding attempts), I am confident that the blue-green female was the mate of the male. It is unlikely that the copulation between the male and brown female was between a male and a secondary mate because none of the 78 breeding attempts in which both males and females were uniquely color marked was polygynous.

On 12 June 1982, I observed a male and female feeding their brood of two 13-day-old nestlings. Both male and female were color marked. Observations began at 11:03. At 11:36 an unmarked male copulated with the female on the nest box top. The copulation was not forced. At the time the resident male was out of view, presumably foraging. The copulating male was unmarked, indicating that he was not a paired breeder at my study site because all known breeders were color marked. Mated pairs were often seen copulating after incubation had begun. One pair even copulated after their eggs had hatched. Why a female would copulate with a male not her mate when her nestlings were 13 days old is not apparent. Tree Swallows never had second broods at my study site. Power and Doner (Am. Nat. 116: 689–704, 1980) suggest several reasons for copulation after the fertilizable period.

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MICHAEL P. LOMBARDO, *Dept. Biological Sciences, Rutgers Univ., P.O. Box 1059, Piscataway, New Jersey 08854.* *Received 19 Mar. 1985, accepted 25 June 1985.*

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**Polygyny in the Yellow Warbler.**—Observations of polygynous matings in Parulinae are rare. Ford (Curr. Ornithol. 1:329–356, 1983) lists 12 species of North American Parulinae, including the Yellow Warbler (*Dendroica petechia*), that are reported to practice polygyny. S. G. Sealy (pers. comm.) and coworkers have noted two apparent cases of polygynous Yellow Warblers at their study site near Delta Manitoba. Here, I report detailed observations of color-marked birds to verify the existence of polygyny in Yellow Warblers and compare the behavior of polygynous and monogamous males.

Yellow Warblers were studied in 1980 and 1981 at the University of Michigan Dearborn Biological Station (Wayne Co., MI) and in 1981 at Metrobeach Metropark (Macomb Co., MI). Birds were banded with U.S. Fish and Wildlife aluminum bands and with celluloid color bands, permitting detailed observations of individuals engaged in territorial disputes and nesting activities. Territories were mapped by following males and plotting the locations of boundary disputes on gridded maps of each study area. I searched daily for all females associated with color-banded males. Observations were kept on nesting behavior and pair-bonds.

Polygyny was observed for Yellow Warblers at Dearborn and Metrobeach. During the two breeding seasons, 21 nesting birds were observed for at least 54 days (Table 1). Three polygynous males were paired with 5 females who built 9 nests. (One of the males was paired with the same female in consecutive years.) Simultaneous associations occurred when polygynous males were paired with females nesting at the same time. When females nested

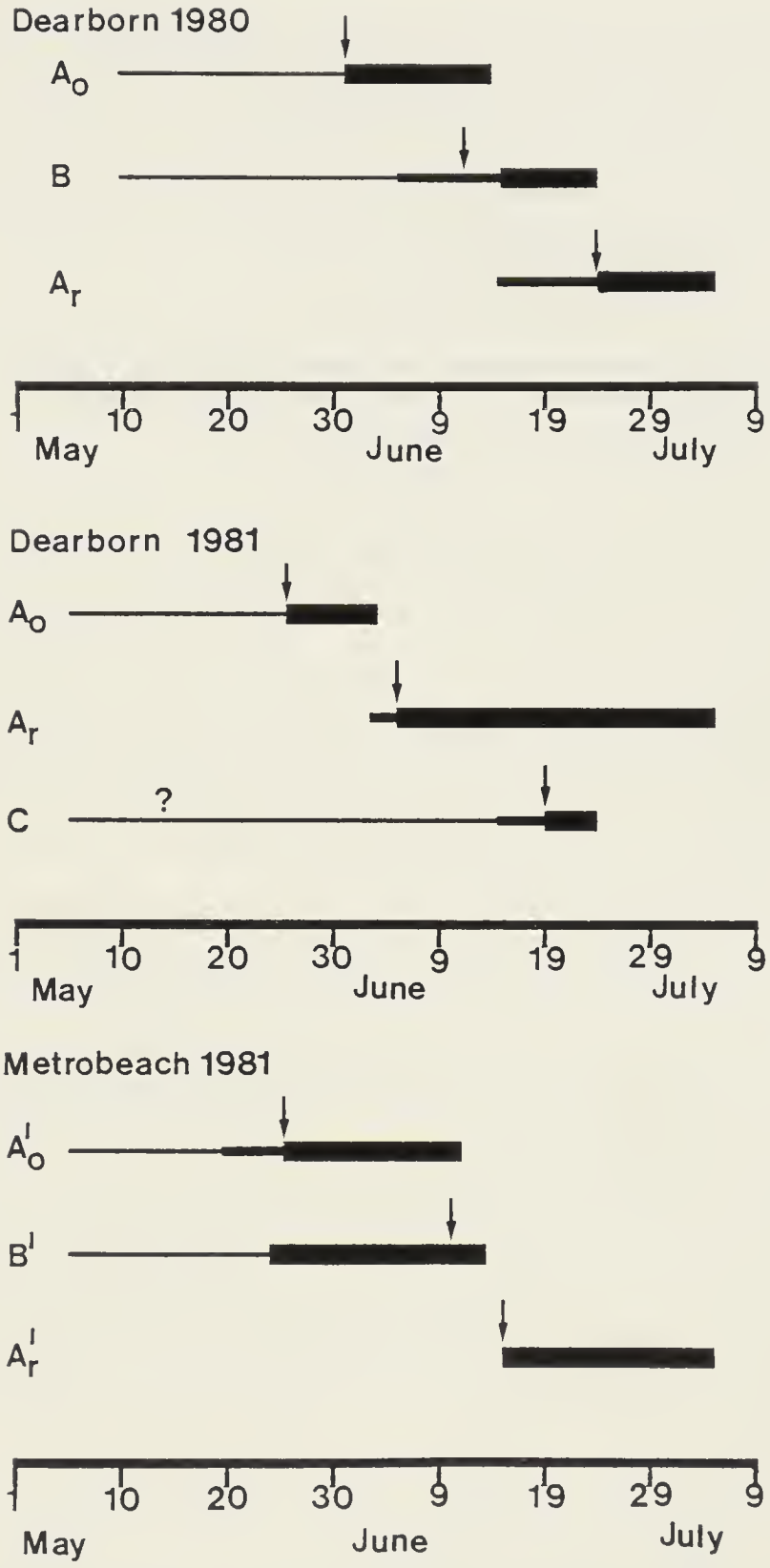
TABLE 1

OBSERVATIONS OF POLYGYNOUS YELLOW WARBLERS AT DEARBORN AND METROBEACH, MICHIGAN, 1980–1981

| Location | Year | Observation period (days) | Duration of simultaneous associations | Male behavior during associations |
|---|---|---|---|---|
| Dearborn | 1980 | 60 | 17 June–7 July | Feeding female |
| | 1981 | 54 | 17 June–25 June | Feeding young<br>Territory defense |
| Metrobeach | 1980 | 62 | 28 May–7 July | Alarm calls |

→

FIG. 1. The breeding period of polygynous Yellow Warblers at Dearborn and Metrobeach, Michigan, 1980–1981. Thin lines represent time females were on the breeding site prior to nesting. Medium lines are based on presumed nesting activities obtained by dating




backwards to nest initiation (see Goossen and Sealy, Can. Field Nat. 96:189–199, 1982). Thick lines represent time a nest was under observation. Arrows indicate when males were first seen with females. Subscript o = an original nest; r = a replacement; ? = the period when a female was not observed on territory.

asynchronously, males directed most of their activities to females that nested first. Males switched their efforts to the second female when the breeding attempt of the first female failed or when her young fledged.

In 1980, two females (A and B) were associated repeatedly with a male (AB) at the Dearborn locality (Fig. 1). The nesting activities of these two females were synchronized from 7 June through 23 June. Following the apparent predation of female A's nest on 13 June, male AB spent most of his time with female B. On 23 June, when female B's young fledged, male AB was found with female A at her replacement nest.

Male AB and female A returned to Dearborn in 1981, and were once again paired (Fig. 1). Male AB was associated with female A and her original nest from 25 May through 2 June, and with her replacement attempt from 6 June through 27 June. On 19 June, male AB was also observed with another female (C), who nested unsuccessfully. The location of this female prior to the discovery of her nest was unknown.

Polygyny was also witnessed at Metrobeach in 1981. A male (AB′) was repeatedly and simultaneously associated with two females (A′, B′) (Fig. 1, Table 1). Associations with female A′ included two breeding attempts (from 28 May through 10 June, 13 June through 7 July). Male AB′ was also observed with female B′ from 10 June through 12 June. This nest was parasitized by a cowbird (8 June) and deserted on 12 June. No further breeding attempts were made by female B′.

Yellow Warblers maintained type A territories (Nice, Am. Midl. Nat. 26:441–487, 1941); however, several males were observed off territory singing near females. Wandering behavior, also observed by M. R. Lein (pers. comm.), Ford (1983), and Nolan (Ornithol. Monogr. 26, 1978) for Prairie Warblers (*D. discolor*), was most prevalent during the incubation period of each male's first mate (pers. obs.). Territory size of polygynous males ($\bar{x}$ = 0.78 ha, N = 3) was significantly greater than that of monogamous males ($\bar{x}$ = 0.21 ± 0.05 ha [SD], N = 20; Mann Whitney $U = 59$, $0.002 < P < 0.005$).

Productivity (no. young fledged per breeding bird) was higher for polygynous males ($\bar{x}$ = 3.67 ± 0.33, N = 3), and females mated to polygynists ($\bar{x}$ = 1.83 ± 0.70, N = 6) than for monogamists ($\bar{x}$ = 1.40 ± 0.36, N = 20). The difference was significant for males ($\chi^2 = 6.97$, df = 1, $P < 0.01$) but not for females ($\chi^2 = 0.458$, df = 1, $P > 0.25$).

Nolan (1978) found that polygynous Prairie Warblers acquired first mates earlier than their monogamous counterparts, and that instability of sex bonds was associated with a high incidence of nest mortality due to predation. In this study, polygynists claimed territories first and then were apparently selected first by females.

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**Two male Bobolinks feed young at the same nest.**—Male "helpers at the nest" have been reported for many species of birds (Brown, Am. Zool. 14:63–80, 1974; Woolfenden, Proc. Int. Ornithol. Congr. 16:674–684, 1976; Emlen, pp. 245–281 *in* Behavioral Ecology, J. R. Krebs and N. B. Davies, eds., Sinauer, Sunderland, Massachusetts, 1978); however, this

situation has rarely been reported for species that are generally regarded as polygynous. Beason and Trout (Wilson Bull. 96:709–710, 1984) described the first case of this phenomenon in an unmarked population of Bobolinks (*Dolichonyx oryzivorus*). Here, we describe a second situation in which two male Bobolinks simultaneously fed young at the same nest. In addition, we present electrophoretic phenotypes for all members of this "family."

The nest was in a 19-ha upland hayfield 6.4 km south of the Cornell Biological Field Station near Bridgeport, New York. The field contained a dense breeding population of Bobolinks. Fifty of 52 (96%) territorial males and 54 of 56 (96%) nesting females were individually color marked. In addition, we took blood samples for electrophoretic analysis from each adult that we captured and from all nestlings that survived to day 7 (Gavin and Bollinger, Auk 102:550–555, 1985). A "two-male" nest was found with a complete clutch of 4 eggs on 28 June 1984, in the territory of O (orange) male. His territory was directly adjacent to territories of trigamous, bigamous, and monogamous males. The attendant female was captured at the nest and marked as Y (yellow) on 2 July. The eggs hatched on 8 July. We observed feeding trips at this nest daily from 9 July through 17 July (when the young fledged) for a total of 8 h (N = 151 feeding trips). From 9 July through 11 July, only O male and Y female fed young at this nest. The second male first fed young on 12 July and continued to feed until after the young had fledged. On 13 July, we captured the second male as he attempted to feed the nestlings. This male (marked W, white) made 17% (26 of 151 trips) of all observed feeding trips to this nest, O male made 36% (54 trips), and Y female was responsible for the remaining 47% (71 trips). On the two days before fledging, W male made 23% of the feeding trips and O male made 27%. Four young fledged from the nest on 17 July and the three adults continued to be seen together in the vicinity of the nest until 22 July. We never observed any aggression between the two males and on several occasions they arrived together at the nest and both perched on a stake placed 2 m from the nest.

The help of the second male may have increased the success of the nest as it fledged the highest number of young (4) of the 9 nests fledging young in July. Conditions for rearing young appeared to be more difficult at this time, when a median number of 2 young fledged from 9 successful nests, compared with a median of 5 young from 29 successful nests in June ($P < 0.001$, Mann-Whitney $U$-test).

Why W male fed young at this nest is unclear, but several explanations are possible. Firstly, he may have sired some of the nestlings at this nest. For example, Y female may have arrived at our site carrying viable sperm from W male after they were unsuccessful at another site. Clutches sired by more than one male have been documented conclusively in this species (Gavin and Bollinger 1985). Electrophoretic analyses indicated that W male did not father two of the nestlings. The data also strongly suggest that O male fathered the two nestlings because of the presence of a rare allele in each of the three birds. This allele was present in 8% of this population, and only 3 of the other 49 marked males had the allele. Either male could have fathered the other two nestlings. We assumed that intraspecific nest parasitism did not occur and that Y female was the mother of all nestlings in her nest (Gavin and Bollinger 1985). Secondly, W male may have been an offspring from the previous year of one or both of the other adults and not a father of any of the nestlings. The electrophoretic data do not exclude this possibility, and helpers at the nest in other species are often male offspring from previous clutches (e.g., Pinkowski, Auk 92:801–802, 1975; Woolfenden 1976). Thirdly, W male simply may have made a "reproductive mistake" (Power, Science 189: 142–143, 1975; Pinkowski, Auk 95:606–607, 1978). He may have still been physiologically motivated to feed young after a recent nest loss (Beason and Trout 1984). Obvious reproductive mistakes (e.g., feeding young of another species) have been described for other species of birds (Shy, J. Field Ornithol. 53:370–393, 1982).

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**Conspecific nest takeovers and egg destruction by White Ibises.**—This report describes cases of conspecific nest usurpation seen in a breeding colony of White Ibises (*Eudocimus albus*) during four breeding seasons (1980–1983) on a 9 ha island in Winyah Bay, near Georgetown, South Carolina (33°16′30″N, 79°12′30″W). Between 6000 and 12,000 pairs of ibises nest there annually on clumps of needlerush (*Juncus roemarianus*), and nests are subject to occasional catastrophic washouts by high tides. My observations, which lasted 12–14 h a day, were made from a 3-m high blind set approximately 20 m from groups of 20–50 nesting pairs. Individuals could be identified reliably by facial characteristics, and sexes were determined by behavior and size (Kushlan, Wilson Bull. 89:92–98, 1977). Over the four seasons, 15,580 pair-h were spent observing 134 pairs during courtship, nestbuilding, egg laying, and occasionally early incubation. For a more detailed description of the study site and methods, see Frederick (Ph.D. diss., Univ. North Carolina, Chapel Hill, North Carolina, 1985).

During these observations, I saw eight cases of nest takeover, all of which involved a similar sequence of events. Without apparent warning, a pair that had built a nest would begin to jab with their bills at a lone female on a nearby nest (<3 m). The lone female (resident) would not attack the intruders, but instead she would spread her wings over the nest cup and lie prone with her head behind her wing. The attacks continued for 15–30 min, during which time the intruding pair jabbed the resident's head, back, neck, and wings hard enough to draw blood and remove contour feathers. The intruding female sometimes appeared to be jabbing underneath the prone resident. In one case a resident female appeared to have been beaten into an unconscious state after >30 min of attacks. The resident female was forced from her nest in five of the eight encounters.

If the resident was evicted, the intruders immediately occupied the nest; if eggs were present, the intruding female stabbed them with her bill and threw them out of the nest. The intruding pair usually rearranged the nesting material and in two cases copulated on the nest within 10 min of the eviction.

In all cases the mate of the resident female returned within 30 min of the eviction and attempted to chase off the intruders. He was always joined by his mate as soon as he returned. In the ensuing fight, males fought males and females fought females. Jabs were aimed at the head, and contestants frequently held each other's throats tightly clamped for several min at a time. The resident pair always chased off the intruding pair after a 20–30-min fight. Contested nests failed in all four of the cases in which their fates were followed.

All initial attacks were made by the intruding female, with her mate following. In two cases, the intruding female also remained fighting on the nest for at least 5 min after the intruding male had given up.

Interpretation of this behavior is difficult. Intruders may have been seeking a new nest site. The colony has a remarkably uniform nesting substrate, however, and nest sites did not appear to be limited, nor did contested nest sites appear to be safer or more productive. Washouts by high tides on the island accounted for a minimum of 75% nest mortality over the four seasons; low nests were a distinct liability. In five of the eight observed cases, however, the intruder's original nest site was higher than the victim's. In all cases, the intruder's nest appeared to be fully constructed and capable of holding eggs. It is unclear, then, why the intruders attempted to take over new nest sites.

The intruding female could have been trying to create an opportunity to dump eggs in the victim's nest. Conspecific egg dumping does occur in colonies of White Ibises (Frederick, 1985; Shields, M.S. thesis, Univ. North Carolina, Wilmington, North Carolina, 1985); however, eggs were never laid by the intruding females during attempted nest takeovers.

In all cases the intruding pair had not laid eggs at the time of the attempted eviction, and the residents had laid from one to three eggs. It is possible that the male or female intruder was infertile. In one case the intruders had been paired for at least 9 days, a longer than usual time before eggs are laid (pers. obs.). Pierotti (Am. Nat. 115, 290–300, 1980) suggested that conspecific chick destruction in Herring Gulls (*Larus argentatus*) was an attempt by unsuccessful nesters to increase their fitness by lowering the fitness of successful neighbors. Intruding pairs of ibis did not attempt to attack more than one nest, however, and the relative increase in the intruder's fitness as a result of only one attack in such a large population is infinitesimally small. Further, if egg destruction were the only purpose of the attacks, intruders should not have attempted to retain ownership of the nest.

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**Winter diets of vultures in southcentral Pennsylvania.**—Except for recent studies by Coleman and Fraser (p. 14 *in* Ann. Meet. Raptor Res. Found., Blacksburg, Virginia, 1984) and Paterson (Wilson Bull. 96:467–469, 1984), information on diets of Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) has been either anecdotal or qualitative. The presence of a large winter communal roost occupied by both of these species at Big Round Top, Gettysburg National Military Park, Adams County, Pennsylvania (Wright, M.S. thesis, Pennsylvania St. Univ., University Park, Pennsylvania, 1984) provided a convenient opportunity to examine winter diets of vultures.The Big Round Top roost was approximately one ha in size. Major overstory trees consisted of white pine (*Pinus strobus*) (42%) and northern hardwoods (birch [*Betula* spp.], maple [*Acer* spp.], and American beech [*Fagus grandifolia*]) (58%), but only white pines were used as roost trees by vultures (Wright 1984). Mean number of vultures at this roost during midwinter was 719 in 1982–83 and 420 in 1983–84. Turkey Vultures and Black Vultures comprised 70% and 30%, respectively, of the totals each year (Wright 1984). We had no evidence to suggest that the two species were segregated within the roost. A variety of different food resources was expected to be available to vultures because Adams County is composed of about 32% forest and 60% farmland. Our objectives were to compare diets of vultures at the Big Round Top roost (1) during two winters that varied in weather severity, (2) during snow-free periods and snow-covered periods of winter, and (3) with those reported for *C. aura* in Virginia.

Sixty-three and 94 pellets were gathered at the roost from late December through February

TABLE 1

PERCENT OCCURRENCE OF ANIMAL FOOD ITEMS PLACED IN FOUR GROUPS BASED ON 157 VULTURE PELLETS COLLECTED AT THE BIG ROUND TOP ROOST, ADAMS CO., PENNSYLVANIA, IN WINTERS 1982–83 AND 1983–84

| Food item | Occurrence |
|---|---|
| Domestic Mammal | |
| Cow (*Bos taurus*) | 22.3 |
| Sheep (*Ovis aries*) | 15.9 |
| Pig (*Sus scrofa*) | 15.9 |
| Subtotal | 54.1 |
| Deer | |
| White-tailed Deer (*Odocoileus virginianus*) | 45.2 |
| Poultry | |
| Chicken (*Gallus gallus*) and Turkey (*Meleagris gallapavo*) | 49.0 |
| Small mammal | |
| Virginia Opossum (*Didelphis virginiana*) | 8.9 |
| Norway Rat (*Rattus norvegicus*) | 2.5 |
| Eastern Cottontail (*Sylvilagus floridanus*) | 1.9 |
| Striped Skunk (*Mephitis mephitis*) | 1.3 |
| Gray Squirrel (*Sciurus carolinensis*) | 0.6 |
| Red Fox (*Vulpes vulpes*) | 0.6 |
| Subtotal | 15.9 |

in 1982–83 and 1983–84, respectively. The pellets egested by the two species of vultures could not be separated because of similarities among pellets collected and a lack of a published guide. Thus, we pooled data from both species. Pellets were air-dried, then separated with a dissecting scope into different types of animal hairs, plant material, and miscellaneous material, including bone fragments and soil. Species identity of each type of animal hair separated macroscopically was identified by preparing impressions of the cuticular scale patterns of at least three randomly selected hairs (Williamson, J. Mammal. 32: 462–464, 1951). The impressions were examined through a compound microscope and compared to reference slides and a hair guide (Adorjan and Kolenosky, Ontario Dept. Lands For. Res. Rep., 90, 1969). All recovered feathers were white and presumed to be either domestic chicken (*Gallus gallus*) or domestic turkey (*Meleagris gallapavo*). Both species of poultry were abundant in Adams County (U.S. Census Bureau, 1982 Census Agric. Preliminary Rep., 1983). Only the occurrence, not the species, of plants in individual pellets was noted because ingestion of plants by vultures may be accidental (Paterson 1984).

Animal food items were placed into one of four groups: domestic mammal, deer, poultry, and small mammal. The frequency of occurrence of food items from each group was compared in diets between winters and between snow-free and snow-covered periods using 4 × 2 tests of independence (Sokal and Rohlf, Biometry, 2nd ed., Freeman, San Francisco, California, 1981). Also, the number of pellets containing a food item versus the number without that food item were compared between winters and between snow-free and snow-

TABLE 2

PERCENT OCCURRENCE OF FOOD ITEMS BASED ON 142 VULTURE PELLETS COLLECTED AT THE BIG ROUND TOP ROOST, ADAMS CO., PENNSYLVANIA, DURING SNOW-FREE PERIODS (<7.6 CM SNOW COVER) AND SNOW-COVERED PERIODS (≥7.6 CM SNOW COVER) IN WINTERS 1982–83 AND 1983–84

| Group[a] | Occurrence | |
|---|---|---|
| | Snow-free period (N = 67) | Snow-covered period (N = 75) |
| Domestic mammal | 47.8 | 53.3 |
| Deer | 40.3 | 45.3 |
| Poultry | 35.8 | 63.7 |
| Small mammal | 20.9 | 9.3 |

[a] Species comprising each group are given in Table 1. Fifteen pellets were omitted because they could not be placed into either the snow-free or the snow-covered period.

covered periods, using 2 × 2 tests of independence. The proportion of each food item in individual pellets was not noted because these data do not necessarily indicate the importance of that item in vulture diets because of (1) differences in biomass among food items and (2) variable ingestion rates of different food items (see Paterson 1984). We feel, however, that our data provide information on the relative abundance of potential food types available to vultures.

Mean January temperature was −0.1°C in 1983 and −3.8°C in 1984 (Wright 1984). Mean daily snow cover was 4.3 cm and 2.3 cm from mid-December through February in 1982–83 and 1983–84, respectively. Snow-free periods were defined as periods when snow depths were less than 7.6 cm, because most carcasses of small food items (e.g., poultry and small mammals) would be covered when snow depths were ≥7.6 cm.

Dry weight of pellets was 1.99 ± 0.62 g (SD); pellets typically were 4.5 cm long, 2.5 cm wide, and 2.0 cm deep at their thickest parts. Eleven animal species were identified in the 157 pellets pooled over the two winters (Table 1). Evidence of domestic mammals, deer, and poultry was noted frequently, whereas hair from small mammals was uncommon. Unidentified hair was found in four pellets. Plant material was present in 27% of the pellets; large amounts of vegetation (>10% total volume) were noted in 5% of the pellets.

Vulture diets did not differ between winters ($G = 1.06$, df = 3, $P > 0.50$) but varied between snow-free and snow-covered periods ($G = 7.36$, df = 3, $0.05 < P < 0.10$) (Table 2). Occurrence of the largest food items, i.e., domestic mammals and deer, in pellets was similar regardless of snow depth ($G \leq 0.38$, df = 1, $P > 0.90$). These larger carcasses were probably conspicuous to foraging vultures by sight or smell (see Rabenold, pp. 303–321 *in* Vulture Biology Management, S. Wilbur and J. A. Jackson, eds., Univ. Calif. Press, Berkeley and Los Angeles, California, 1983), except under excessive snow cover. Snow depth never exceeded 74 cm during either winter at the Big Round Top roost. The frequency of poultry diets, however, was greater during snow-covered than during snow-free periods ($G = 10.32$, df = 1, $P < 0.01$). This suggests that vultures depend more on farms with abundant and predictable sources of poultry carcasses during periods of snow cover. The occurrence of small mammal remains in pellets tended to decline during snow-covered periods ($G = 3.78$, df = 1, $0.05 < P < 0.01$).

We compared our results to autumn diets of Turkey Vultures in Montgomery County, Virginia (Paterson 1984). The occurrence of domestic mammal hair was high in both studies;

however, sheep hair occurred more often (55%) in the Virginia study, whereas cow hair predominated in our study (Table 1). This difference probably was due to availability rather than to dietary preferences. In Adams County, during 1982, cows outnumbered sheep 10 to 1 (U.S. Census Bureau 1983); in Montgomery County, during 1978, cows outnumbered sheep only 5 to 1 (U.S. Census Bureau, 1978 Census Agric. Preliminary Rep., 1978). Virginia vultures consumed more poultry than those in Pennsylvania, with feathers occurring in 70% of the pellets compared to 49% in the present study (Table 1). But poultry availability, based simply on numbers per county, did not explain the difference between studies because chickens, for example, were over 200 times more abundant in Adams County than in Montgomery County (U.S. Census Bureau 1978, 1983). Deer hair occurred less often (32%) in the Virginia pellets (Paterson 1984) than in the Pennsylvania pellets (Table 1). Deer harvest and road-kills are relatively high in Adams County (Wright 1984; H. Greenlee, pers. comm.). Vultures regularly fed on deer carcasses near the Big Round Top roost during winter (Coleman and Fraser 1984).

Finally, although shrews (Soricidae) and moles (Talpidae) were noted in 23% and 27%, respectively, of the autumn pellets in Virginia (Paterson 1984), all small mammals combined were represented in only 16% of the Pennsylvania pellets. However, when only pellets collected during the snow-free period in Pennsylvania were considered, the occurrence (21%) of small mammals in pellets (Table 2) was similar to that reported in Virginia. Snow cover may have a greater impact on food resources of Turkey Vultures than those of Black Vultures in our study; Coleman and Fraser (1984) observed Turkey Vultures feeding at small carcasses more often than did Black Vultures.

The result of our pellet examination indicates that vultures are opportunistic scavengers during winter. The diverse food available in southcentral Pennsylvania, together with the presence of suitable roosting habitat (Wright 1984), probably contributes to the current abundance of Black and Turkey Vultures in southcentral Pennsylvania.

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**Breeding Biology of the Seychelles Black Parrot (*Coracopsis nigra barklyi*).**—The Seychelles Black Parrot (*Coracopsis nigra barklyi*) is endemic to the island of Praslin in the Seychelles. It is listed as rare in the Red Data book (King, ICBP, Washington, D.C., 1978). Previous studies of the endemic birds of the Seychelles have called for additional information on the islands' rare and endangered species (Vessey-Fitzgerald, J. Ecol. 28:465–483, 1940; Loustau-Lalane, Occas. Publ. Seychelles Soc. 1:32, 1962; J. Seychelles Soc. 3:64, 1963; Gaymer et al., Ibis 111:157–176, 1969; Penny, Oryx 9:267–275, 1968). The Seychelles Black Parrot was first described by Newton (1867). Other populations of this species occur on the

TABLE 1

NUMBERS OF PARROTS OBSERVED DURING SIMULTANEOUS COUNTS IN 1983 AT SITES WITHIN THE KNOWN RANGE OF PARROTS ON PRASLIN

| Date[a] | Number of observation points | Total number of parrots observed |
|---|---|---|
| 22 Sept. | 13 | 29 |
| 29 Sept. | 13 | 29 |
| 6 Oct. | 13 | 32 |
| 13 Oct. | 13 | 39 |
| 20 Oct. | 13 | 32 |
| 27 Oct. | 13 | 41 |
| 3 Nov. | 13 | 29 |
| 10 Nov. | 20 | 33 |
| 17 Nov. | 21 | 58 |
| 24 Nov. | 21 | 48 |
| 1 Dec. | 20 | 32 |

[a] All counts took place between 08:00 and 08:30 h.

Como Islands and on Madagascar. The present study is intended to add to the limited knowledge of the breeding biology of this species.

*Study area and methods.*—Praslin, the second largest island of the Seychelles archipelago (55°30′E, 4°20′S), is an approximately 41 km$^2$ granitic island located 44 km north of the largest island, Mahé. The island, which is covered with large boulders from the ocean edge up to an elevation of 387 m, is approximately rectangular in shape and has a ridge along the long axis as well as a number of steep valleys. The Valleé de Mai National Park is located in the center of Praslin. It is an area of 100 ha owned by the Republic of Seychelles. The climate of the island is tropical, with a mean temperature of 26.9°C and an average monthly rainfall of 8.1 cm. During the rainy season (October to March) the rainfall averages 30.4 cm per month. A thorough description of the Seychelles Islands is given by Gaymer et al. (1969). The vegetation is described by Vessey-Fitzgerald (1940).

We studied parrots on Praslin from 13 June to 1 August 1982 and from 1 July 1983 through 22 January 1984. We studied parrots throughout Praslin but concentrated our observations in the Valleé de Mai region. With few exceptions, observations of parrots were carried out daily. On 11 occasions we attempted to make simultaneous counts of parrots in as many as possible of 21 locations where we had regularly seen birds. These counts were made from 08:00–08:30 and provide a minimum estimate of the parrot population.

We attempted to capture parrots in 4-in. mesh, 12-m, black-nylon mist-nets placed at various locations where parrots had been seen feeding. We set nets near the ground and also at forest-canopy heights by using pulleys attached to bamboo poles. All open nets were monitored continuously.

We discovered four active nesting areas in the Valleé de Mai. In 1983 we monitored three active nests and obtained information on nest location, clutch size, hatching and fledging success, and growth rates of nestlings.

*Results.*—Counts of parrots ranged from 29 to 58 (Table 1). The minimum size of the population must be greater than 58, but we do not know how many more birds there might have been. Two birds were caught in mist nets placed near Bilimbi trees (*Averrhoa bilimbi*) where the birds had been seen feeding. It was impossible to sex or age the birds, but weights

TABLE 2
MEASUREMENTS AND DESCRIPTION OF TWO LIVE PARROTS CAUGHT IN MIST NETS

| | Date of capture | |
|---|---|---|
| | 29 Aug. 1983 | 9 Nov. 1983 |
| Wing chord (mm) | 167 | 186 |
| Tail length (mm) | 119 | 130 |
| Culmen length (mm) | 23 | 19 |
| Tarsus length (mm) | 18 | 19 |
| Weight (g) | 153 | 140 |
| Eye color | Brown | Brown |
| Bill color | Bone | Bone |

and other measurements were taken (Table 2). In general, these measurements are within the ranges given by Forshaw (Parrots of the World, Lansdowne, Melbourne, Australia, 1973: 584).

Prior to our study only two nests had been described (Lousteau-Lalanne 1963). These nests were in trees that were broken at the top and were hollow. Using the descriptions of nest trees by Lousteau-Lalanne as a guide, in 1982 we counted the number of potential nest trees on 100 ha in the Valleé de Mai and found 45 dead, hollow, broken trees that had hollow trunks deep enough for parrots to nest. At Fond Ferdinand we found only two trees in a 25-ha area. The Fond Peper area of 80 ha yielded nine Coco de Mer Palms (*Lodoicea maldivica*) that were hollow and broken off. Fond Badimier had two such trees in 20 ha. The results of our survey suggested that Coco de Mer Palms alone are sufficiently numerous to satisfy the nesting needs of the parrots. Potential nest cavities also exist in other species of trees and in areas not included in our surveys, which covered only a small percentage of the total area of nesting habitat available on the island. All known nests, however, have been located in the areas we surveyed.

We observed a parrot leaving a dead, hollow Coco de Mer Palm in the Valleé de Mai on 16 November 1982. The nest was at the base of the hollow tree and 3.6 m below the entrance to the cavity (Table 3). The first egg was found in the nest on 17 November 1982. The second egg was found a day later. Both eggs hatched on 6 December 1982 after an 18-day incubation period. One young parrot fledged on 11 January 1983, and the other left the nest on 24 January 1983.

The first nest of 1983 was found on 20 December at the same site used in 1982. The nest contained a single egg that was laid between 11:11 and 11:22 while we were monitoring the nest. On 23 December 1983 the egg was found broken. On 26 December 1983 a new egg was discovered in the nest; no additional eggs appeared. Observations at this nest revealed the method used by the parrot to descend into the deep cavity. The parrot would alight on the edge of the upward-facing cavity entrance and then lean forward to grasp the opposite edge with its bill; it would then swing its feet to the inside of the cavity and back down to the base of the cavity. When leaving it climbed up the inside of the trunk.

The second nest of 1983 was found in the Valleé de Mai in a Coco de Mer Palm (Table 3). This nest contained three eggs, which were being incubated at the time of discovery. No additional eggs appeared in the nest.

On 5 January 1984, a third nest was found in the Valleé de Mai. The nest was in a hollow trunk of a dead Albizzia tree (*Albizzia falcatoria*). At the time of discovery the nest contained

TABLE 3
DESCRIPTIONS OF PARROT NESTING TREES AND NEST CAVITIES LOCATED IN THE VALLEÉ DE MAI

| | Nest site | | |
|---|---|---|---|
| | A | B | C |
| Type of tree | Coco de Mer | Coco de Mer | *Albizzia* |
| Height of tree (m) | 4 | 5.9 | 2.5 |
| Cavity depth (m) | 3.6 | 1.5 | 1.8 |
| Inside diameter of cavity (cm) | 26 | 24.5 | 2.3 |

a broken egg and one newly hatched young. The nest was 80 m northwest of nest B and 115 m northeast from nest C (Table 3). On 11 January 1984, the young in the nest was found freshly dead and partially eaten. We suspect that a rat (*Rattus rattus*) was the predator.

The parrot eggs we examined were white and oval in shape. Prior to our study only one egg had been described (Forshaw 1973). That egg measured 38.6 × 30.5 mm. Our eggs measured: $\bar{x}$ length = 35.8 mm, range = 31–40 mm; $\bar{x}$ width = 26.4 mm, range = 25–34 mm; N = 5. Clutch size varied between 2 and 3 eggs per nest. Out of the total of 9 eggs we observed, 3 eggs were destroyed before hatching, and one egg was infertile. The nesting season began in November when the first eggs were laid and lasted until February when the last chick fledged.

The single chick in nest C was weighed on three consecutive days at 10:30. It weighed 82 g when 15 days old, 67 g when 16 days old, and 70 g when 17 days old.

*Acknowledgments.*—The senior author wishes to acknowledge Indiana Univ. of Pennsylvania for granting him a sabbatical leave from 1 July 1983 to 1 July 1984. International Business Machines and L. Zambotti made financial contributions to this research project. The government of the Republic of Seychelles is acknowledged for its support of fieldworkers S. M. Savy and L. Chong Seng.—ROBERT E. MERRITT, *Dept. Biology, Indiana Univ., Indiana, Pennsylvania, 15705,* PATRICIA A. BELL, *P.O. Box 445, Indiana, Pennsylvania, 15701,* AND VICTORIN LABOUDALLON, *Dept. Forestry and Conservation, Fond Boffay, Praslin, Republic of Seychelles.* *Received 15 Feb. 1985, accepted 21 June 1985.*

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**Additions to records of North American avifauna in Yucatán, Mexico.**—The symposium entitled "Migrant Birds in the Neotropics: Ecology, Behavior, Distribution and Conservation" (Keast and Morton, eds., Smithsonian Inst. Press, Washington, D.C., 1980) contained numerous statements concerning our lack of knowledge about bird migration in Central America and Mexico. Since 1979, we have made an effort to learn more about the distribution of migratory birds and their times of arrival by use of mist nets. We have not been able to approach this project in a systematic way because much of the work has been done by personnel whose time was donated by the government of Mexico at locations that were expedient. The data contained herein were gathered at eight locations (Fig. 1) from 16 September 1981 through 1 December 1983 at various times of the year and with various numbers of nets.

The study area lies north of 20°15′N and, except for El Cuyo (21°30′N, 87°10′W), between

TABLE 1

MIGRATORY BIRDS TRAPPED IN YUCATÁN DURING FALL AND SPRING 1981 AND FALL AND WINTER 1982 AND 1983

| Species | Dates | Locations[a] | No. caught |
|---|---|---|---|
| Yellow-billed Cuckoo (*Coccyzus americanus*) | 16, 19, 27 Sept.; 7, 9, 13, 19 Oct. | 1, 3 | 6 |
| Black-billed Cuckoo (*C. erythropthalmus*) | 5 Oct.[b] | 1 | 1 |
| Ruby-throated Hummingbird (*Archilochus colubris*) | ? | 1 | ? |
| Acadian Flycatcher (*Empidonax virescens*) | 10 Jan.; 11 Mar.; 6 Oct.[b] | 1, 8 | 2 |
| Least Flycatcher (*E. minimus*) | 26 Sept.; 6, 8 Oct. | 1 | 2 |
| Yellow-bellied Flycatcher (*E. flaviventris*) | 2, 5 Oct.[b] | 1 | 2 |
| Eastern Wood-Pewee (*Contopus virens*) | 30 Sept. | 1 | 5 |
| Great Crested Flycatcher (*Myiarchus crinitus*) | 16 Sept.; 12 Oct. | 1 | 2 |
| Gray Catbird (*Dumetella carolinensis*) | 9, 13 Mar.; 4 Oct.;[c] 11, 17 Nov. | 1, 7, 8 | 8 |
| Swainson's Thrush (*Catharus ustulatus*) | 25 Sept.[b] | 1 | 1 |
| Red-eyed Vireo (*Vireo olivaceus*) | 27 Sept.; 10 Oct. | 1 | 2 |
| White-eyed Vireo (*V. griseus*) | 12, 22 Jan.; 10, 11 Mar.; 9 Aug.;[b] 4, 6, 12, 14, 19 Oct.; 1, 6, 10, 14, 17 Nov. | All | 24 |
| Prothonotary Warbler (*Protonotaria citrea*) | 19 Sept.[c] | 1 | 1 |
| Blue-winged Warbler (*Vermivora pinus*) | 16 Sept.;[b] 6 Oct.[b] | 1 | 3 |
| Lawrence's Warbler (*V. pinus* × *chrysoptera*) | 5 Oct.[b] | 1 | 1 |
| Tennessee Warbler (*V. peregrina*) | 9, 27 Aug.; 4, 6, 7, 9, 12, 13, 16, 21 Oct.; 2 Nov. | 1, 2, 3 | 45 |
| Northern Parula (*Parula americana*) | 10, 18 Jan.; 10 Aug.;[c] 11 Oct. | 1, 3, 5 | 7 |
| Yellow Warbler (*Dendroica petechia*) | 10, 11 Jan.; 9, 27 Aug.;[c] 16 Oct. | 1, 2, 3, 4, 5 | 11 |
| Magnolia Warbler (*D. magnolia*) | 5 Feb.; 9 Mar.; 13 Oct.; 10,[c] 12, 20 Sept.; 4, 5, 6, 8, 13, 15 Oct. | 1, 3, 8 | 30 |
| Yellow-rumped Warbler (*D. coronata*) | 10, 18, 19, 20, 22, 24, 28 Jan.; 1, 10, 17, 19, 22 Feb. 22, 24 Mar.; 12, 19 Apr. | 3 | 217 |

TABLE 1
CONTINUED

| Species | Dates | Locations[a] | No. caught |
|---|---|---|---|
| Black-throated Green Warbler (*D. virens*) | 9 Oct.[c] | 1 | 1 |
| Yellow-throated Warbler (*D. dominica*) | 10 Aug.[c] | 5 | 1 |
| Chestnut-sided Warbler (*D. pensylvanica*) | 25 Sept.;[c] 5, 6, 9, 10, 12 Oct. | 1 | 11 |
| Palm Warbler (*D. palmarum*) | 26 Aug.[b] | 4 | 9 |
| American Redstart (*Setophaga ruticilla*) | 4 Feb.; 19 Sept.[b] | 1, 4 | 3 |
| Black-and-White Warbler (*Mniotilta varia*) | 10 Mar.; 4, 5 Oct.; 17 Nov. | 1, 7, 8 | 6 |
| Ovenbird (*Seiurus aurocapillus*) | 10 Jan.; 9 Aug.,[b] 19, 20, 25, 26, 29 Sept.; 5, 6, 7 Oct.; 17 Nov. | 1, 2, 7 | 18 |
| Northern Waterthrush (*S. noveboracensis*) | 10, 20 Jan.; 12 Mar.; 1,[b] 2, 18 Sept.; 22 Oct. | 1, 3, 4, 8 | 7 |
| Kentucky Warbler (*Oporornis formosus*) | 10 Jan.; 10 Aug.; 2 Sept.; 16 Oct. | 3, 4 | 3 |
| Hooded Warbler (*Wilsonia citrina*) | 5 Feb.; 27 Aug.; 5 Oct.; 16, 18 Nov. | 1, 4, 7 | 12 |
| Common Yellowthroat (*Geothlypis trichas*) | 10 Jan.; 2, 17 Feb.; 10, 13 Mar.; 10, 26 Aug.; 6, 13, 16 Oct.; 20 Nov. | 1, 2, 3, 4, 6, 8 | 30 |
| Summer Tanager (*Piranga rubra*) | 2 Oct.[b] | 1 | 1 |
| Orchard Oriole (*Icterus spurius*) | 18, 19, 20, 22 Jan.; 12 Mar.; 12, 15 Apr. | 3, 8 | 13 |
| Painted Bunting (*Passerina ciris*) | 10, 18, 20 Jan.; 4 Feb.; 10, 12 Mar.; 5 Apr.; 19 Sept. 12, 22 Oct.; 3 Nov. | 1, 3, 4, 8 | 17 |
| Indigo Bunting (*P. cyanea*) | 19, 20, 21, 24, 25, 28 Jan.; 1, 2, 10, 11, 17 Feb.; 18, 19, 21, 22, 24, 29, 30 Mar.; 4, 6, 12, 18, 19, 20, 22, 23, 31 Oct.; 1, 2, 3, 11, 20 Nov.; 1 Dec. | 1, 3, 8 | 381 |
| Blue Grosbeak (*Guiraca caerulea*) | 24, 30 Mar.; 6, 7, 12, 13, 15, 16 Apr.; 15 Oct. | 2, 3 | 11 |
| Rose-breasted Grosbeak (*Pheucticus ludovicianus*) | 12 Mar.; 9 Aug.;[c] 30 Sept.; 4, 11 Oct. | 1, 2, 8 | 6 |

[a] See Fig. 1.
[b] No fall record in Paynter (1955).
[c] Earlier fall record than Paynter (1955).

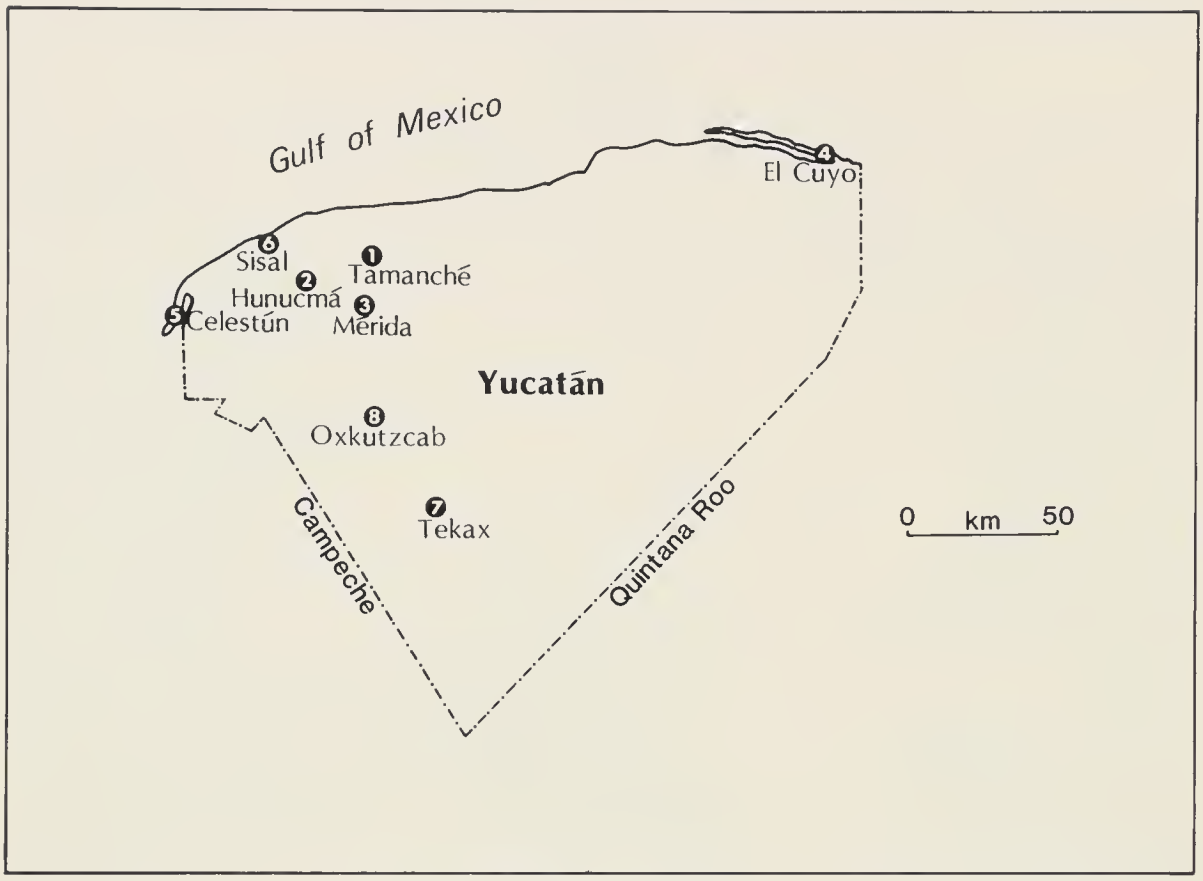


FIG. 1. Netting sites in the State of Yucatán.

89° and 90°W. At Tamanché, an area of open scrub forest, 15 nets (2.3 m × 13.8 m) were opened from 08:00 to 16:00 from 9 September through 12 October 1981 whenever weather permitted. (There were some shortened work days in September due to rain.) In El Vivero (a tree nursery in Mérida consisting of small citrus trees [<2 m]), 15 nets were used from 18 January 1983 through 3 February 1983. The nets were opened from 08:00 to 16:00 whenever weather permitted. This schedule was repeated from 17 February 1983 through 15 April 1983. The other 6 sites were worked opportunistically. The sites at Oxkutzcab were mature orange groves, at El Cuyo the site was a savanna area, and at Celestún nets were set in low second growth next to mangroves. All other sites were open dry scrub forest (<10 m).

When our data are compared with the data of Paynter (Bull. Peabody Mus. Nat. Hist. 9, 1955), it is obvious that many species arrive earlier than had previously been suspected (Table 1). We consider the most unusual records to be the 9 August date for the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Ovenbird (*Seiurus aurocapillus*). Data from 25 years of tower casualties near Tallahassee, Florida, indicate late September as the earliest record of the Rose-breasted Grosbeak and there is only one early August date for the Ovenbird (Crawford, Bull. Tall Timbers Res. Sta. 22, 1981). Lawrence's Warbler (*Vermivora pinus* × *chrysoptera*) is also notable because we can find no previous record of its occurrence in Yucatán.

From 12 to 31 October 1983, the Indigo Bunting (*Passerina cyanea*) was the most numerous species at El Vivero (Mérida) with 81 individuals netted compared to 31 individuals of all other migrant species combined. No birds were recaptured during October, nor were any Yellow-rumped Warblers (*Dendroica coronata*) netted then, although this species became numerous later in the fall. The fact that no Indigo Buntings were recaptured in October indicates that they are a transient species then.

Daily netting at Tamanché produced a more balanced distribution of species of migrants with 38 Tennessee Warblers (*Vermivora peregrina*) and 126 individuals of all other migratory species combined, not counting the Ruby-throated Hummingbird (*Archilochus colubris*), which we did not band.—DAVID T. ROGERS, JR., *Dept. Biology, Univ. Alabama, University, Alabama 35486,* JESÚS GARCIA B. AND ANTONIO RÓGEL B., *Secretariá de Desarollo Urbano y Ecologia, Mérida, Yucatán, Mexico.* *Received 21 July 1984, accepted 30 July 1985.*

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**Choice of nest boxes by cavity-nesting ducks.**—In an earlier study (Lumsden et al., Wilson Bull. 92:497–505, 1980), we found that both Common Goldeneyes (*Bucephala clangula*) and Hooded Mergansers (*Lophodytes cucullatus*) preferred boxes with entrances of 13 × 10 cm over those with entrances of 10.5 × 8 cm or 7.5 × 6 cm. In that study, entrance holes were cut into inspection plates that were attached to the front of each box. Twice, Common Goldeneyes nested in boxes where the inspection plate had fallen off. Here, we report on goldeneye use (1) of boxes with entrances of 13 × 10 cm (the size chosen in the previous study) vs 21 × 13 cm (the size of entrances without an inspection plate), (2) of boxes with and without nesting material, and (3) of boxes at different heights above the ground.

*Materials and methods.*—The study was conducted at two lakes (Elk and Long) and 2 rivers (Mattagami and Muskego) in eastern Ontario. In 1980–1982 we set out 47–51 pairs of boxes with large (21 × 13 cm) and small (13 × 10 cm) entrance holes on each lake each year. All of the boxes contained wood chips as nest material, and all were mounted at 3 m. In 1984, we put 6 or 7 cm of wood shavings in one box of each pair, leaving the other with a bare wood floor. Fifty sets of boxes were available on each lake.

Between 1977 and 1984, on the Mattagami and Muskego rivers, we tested preferences for boxes placed on the same tree at 3, 4.5, and 6 m above the ground. An average of 20 sets of boxes was available each year, and all contained wood chips and had entrances 13 × 10 cm.

We considered that a box was used if a duck laid one or more eggs in it. The size, shape, and color of the eggs of goldeneyes vary (Dow and Fredga, J. Anim. Ecol. 53:679–692, 1984; Lumsden, unpubl. data) so that it is often possible to tell if two or more females use the same box. In such cases we scored the box as having been used twice. A successful female may return in succeeding years to the same box to nest. To increase the independence of our data, we scored boxes as having been used or not used, and the number of years a box was used was ignored. We inspected boxes once in late May–early June. Sometimes nests had been preyed on, and the box was found with a mass of down and no eggs. We scored such boxes as used.

*Results and discussion.*—The size of entrances did not significantly influence the choice of boxes used by Common Goldeneyes. We recorded 19 uses of boxes with small and 13 uses with large entrances ($\chi^2 = 1.125$, df = 1, $P > 0.05$). Ten Hooded Mergansers used boxes with small entrances, and 3 used boxes with large entrances (Binomial Test, $P < 0.05$). All four Wood Ducks (*Aix sponsa*) used boxes with small entrances. Although Common Mergansers (*Mergus merganser*) are able to squeeze through a small entrance hole, they seldom do so. One bird laid a single egg in a box with a small entrance, completing her clutch in the neighboring box with a large hole. Three other Common Mergansers completed their clutches in boxes with large entrances.

In the test involving nest material, all 18 ducks (10 Common Goldeneyes, 4 Hooded Mergansers, 2 Common Mergansers, and 2 Wood Ducks) using the boxes chose the ones with wood shavings. Common Goldeneye preference for the presence of nest material is clear (Binomial Test, $P < 0.05$).

On the Mattagami and Muskego Rivers, Common Goldeneyes chose the 3 m boxes 3 times, the 4.5 m boxes 9 times, and the 6 m boxes 14 times. This choice pattern differs significantly from a 1:1:1 ratio ($\chi^2 = 7.00$, df = 2, $P < 0.05$). Other species did not nest in this area. Although Common Goldeneyes chose the highest boxes more frequently than the others, the rate of occupancy would probably not change in the absence of choice. In 1975 and 1976, all sets of boxes on those rivers were mounted at 3 m (Lumsden et al. 1980). The rate of occupancy both years was similar to that during the years when boxes of different heights were available (1975–76, mean = 8.5 females, range = 7–10; 1977–84, mean = 7.0 females, range = 3–12).

Mink occasionally prey on goldeneye nests in boxes placed at 3 m, and it is likely that the frequency of nest predation would drop with an increase in the height of the box.

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**Rock Doves nesting in trees.**—Rock Doves (*Columba livia*) are native to the Old World and originally nested in sheltered recesses or caves high on cliffs (Goodwin, Pigeons and Doves of the World, Br. Mus., London, England, 1967). In recent history, Rock Doves have colonized cities around the world, usually nesting on window ledges, in building crevices, and under bridges (Harrison, A Field Guide to Birds' Nests, Houghton Mifflin, Boston, Massachusetts, 1975). This note documents an instance of Rock Doves nesting in trees in Oxford, Butler County, Ohio (pop. 30,000), a town with many tall shade trees that form a partial canopy at 12–15 m.

From 14 to 28 April 1982, I located 54 Rock Dove nests on a 105-ha tract of urban Oxford. Forty-one (76%) of the nests were on buildings; the remaining 13 nests (24%) were in trees. Ten of the tree nests were in enclosed holes; 3 (23%) were in open cavities. Eight of the 15 tree nests were in silver maple (*Acer saccharinum*); 2 (15%) were in white ash (*Fraxinus americanus*); and 1 (8%) each was in sugar maple (*A. saccharum*), American basswood (*Tilia americana*), and black cherry (*Prunus serotina*). Tree nests were 9.1 ± 3.7 m (SD) (N = 12) above ground in trees averaging 22.4 ± 8.0 m (N = 12) tall; the average diameter at breast height (dbh) of nest trees was 77.7 ± 19.5 cm (N = 12).

A random sample (N = 34) of cavity trees in the study area yielded the following tree-species composition: silver maple 62%, sugar maple 21%, and other species 17%. Tree nest distribution did not differ ($\chi^2 = 3.3$, df = 2, $P > 0.05$) from the actual cavity distribution. Cavities in the random sample were located an average of 8.0 ± 3.1 m (N = 34) above ground in trees averaging 19.8 ± 6.1 m (N = 20) tall; average dbh was 72.7 ± 15.5 (N = 20). Nest-tree measurements did not differ ($P > 0.05$) from the random sample. Thus, Rock Doves used tree nest sites according to availability of cavities.

Previous reports of Rock Doves nesting in trees are of small numbers of birds in widely scattered localities (Baker, Indian Pigeons and Doves, Witherby, London, England, 1913;

Ludlow and Kinnear, Ibis 4:95, 1934; Barclay-Smith, Br. Birds 57:517, 1964; Boswall, Bull. Br. Ornithol. Club 93:38–39, 1973). The only previous record of Rock Doves nesting in trees in North America is a brief mention of tree nesting in New York state by Barclay-Smith (1964).

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**A new method for collecting prey delivered to Tufted Puffin chicks.**—The food habits of seabird chicks in general are not well known. A commonly used method of discovering what seabirds eat is to collect adults and examine the contents of their stomachs (e.g., Pearson, J. Anim. Ecol. 37:521–552, 1967; Bedard, Can. J. Zool. 47:1025–1050, 1969; Sealy, Auk

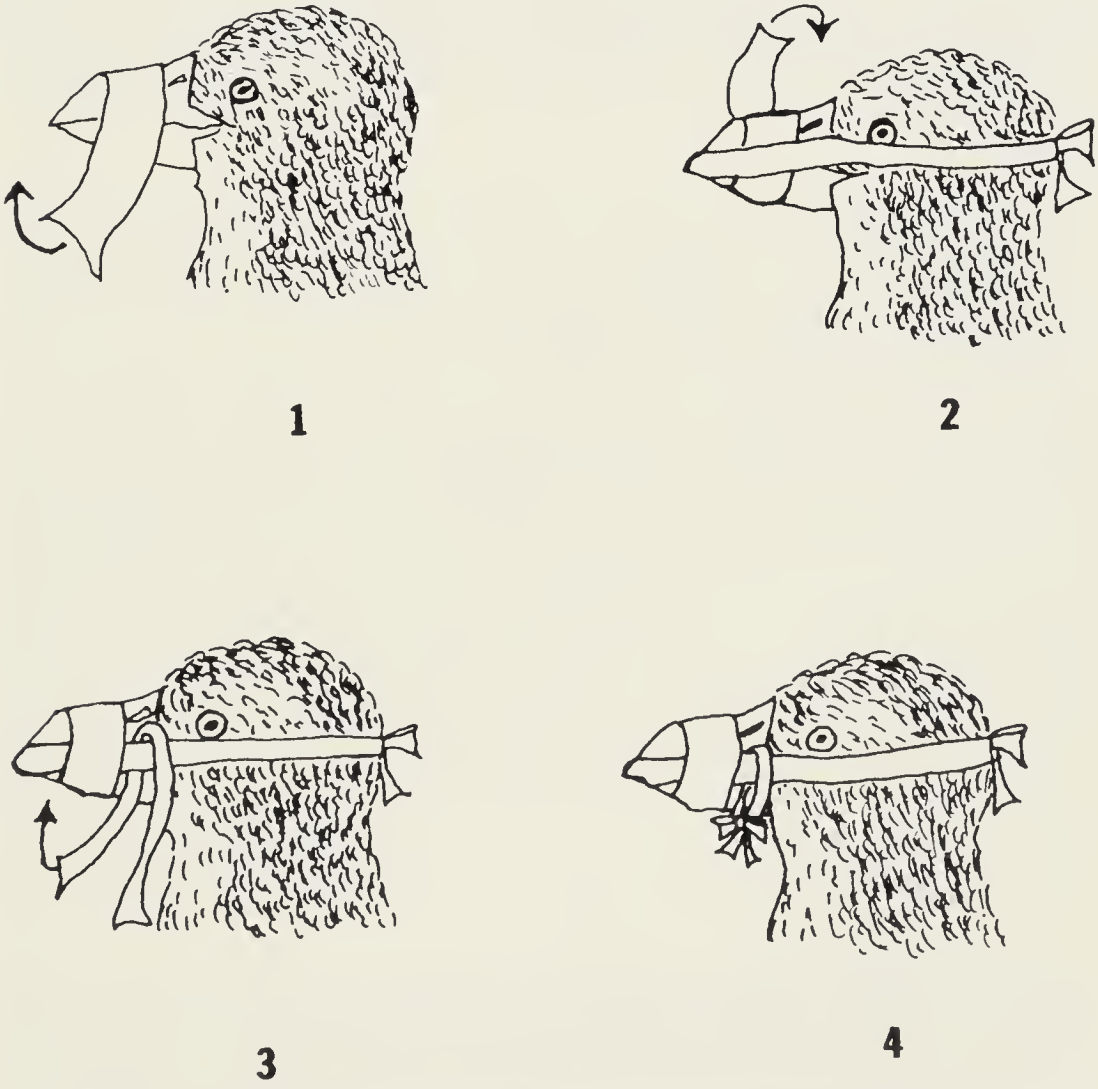


Fig. 1. Sequential steps of tying the bill harness on the Tufted Puffin chick.

90:796–802, 1973; Sanger and Baird, pp. 372–417 *in* Environmental Assessment of the Alaskan Continental Shelf, Final Rep., Vol. 12, NOAA, Environ. Res. Lab, Boulder, Colorado, 1977); however, the collection of breeding adults usually results in the subsequent death of dependent chicks. To segregate food that adults eat from that which they feed to chicks is difficult, if not impossible, except in species that carry food to their chicks in their bills or neck pouches.

Although chicks of some species regurgitate their stomach contents readily, chicks of a number of species do not. For these chicks, other methods to obtain food are necessary. Some investigators have tied string loosely around the neck of the chick, obstructing the passage of food down the esophagus (Orians and Horn, Ecology 50:930–938, 1969), or have inserted a finger down the esophagus of the chick (Hunt, Ecology 53:1051–1060, 1972). In the above methods, regurgitated food is in various stages of digestion, and often whole prey are not involved.

Here, I describe a method to ascertain the prey delivered to Tufted Puffin chicks (*Fratercula cirrhata*). I tested this method on 30 puffin chicks on Kodiak Island, Alaska, in 1977–1978. The method may also be useful on other fish-eating species in which the parents bring back bill loads of prey and drop them on the floor of the burrow. The method consists of placing a bridle on the chick so that the chick cannot swallow food delivered by the adults (Fig. 1). The researcher visits the burrow periodically and removes all prey inside. Prey are usually quite fresh, even after 24 h, so that their weight, volume, and length are close to fresh values. A large sample of chicks should be used for this method, and if an individual is repeatedly sampled, I suggest supplementing its diet with additional food, preferably food that it normally eats.

The bridle may be constructed of plastic bandages or electrical tape for the first wrap and filament tape folded together or surveyor's tape for the harness. The neck harness must be loose enough so that it will not interfere with the chick's respiration. Similarly, the nares should not be taped. I advise checking the chick at 4-h intervals to ensure that the nares do not become clogged with mud. Bridles should be removed at the end of each day, at which time the chicks should be fed.

The method does not physically injure the chick, which can occur with esophageal constriction or the retrieval of food by finger insertion.

*Acknowledgments.*—I would like to thank the National Oceanic and Atmospheric Administration, the Bureau of Land Management, and the U.S. Fish and Wildlife Service for funding the study during which time I developed this method. The research was undertaken while I worked for the U.S. Fish and Wildlife Service in 1977 and 1978. I also thank R. A. Moe for original ideas concerning the development of the bridle. Thanks go to J. Trapp, D. Derksen (USFWS), and G. L. Hunt, Jr. for helpful suggestions, and to referees D. Ainley, S. Sealy, D. Brown, and K. Bildstein for valuable comments in their review of the manuscript.—Pat Baird, *Kahiltna Research Group, "Summerhill," P.O. Box 91316, Anchorage, Alaska 99509.* (Present address: *Dept. Ecology and Evolutionary Biology, Univ. Calif., Irvine, California 92717.*) *Received 24 Apr. 1985, accepted 1 Aug. 1985.*

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**Laughing Gull nesting attempt on Lake Erie.**—On 21 May 1984 we discovered a Laughing Gull (*Larus atricilla*) incubating a single egg in a Ring-billed Gull (*L. delawarensis*) colony on a dredge disposal dike in Maumee Bay, western Lake Erie (Lucas County, Ohio). The nest was at the edge of the dike-top road in the midst of a dense cluster of Ring-billed Gull nests. On 23 May the nest contained two eggs; their measurements were 52.4 × 36.3 mm

and 53.8 × 36.5 mm, respectively. These measurements agree with those given for the Laughing Gull in Bent (Life Histories of North American Gulls and Terns, U.S. Natl. Mus. Bull. 113, 1921), and were less than those of all eight Ring-billed Gull eggs in three adjacent nests (range of egg lengths 54.0–57.2 mm; range of widths 39.5–41.3 mm). Thus we conclude the eggs were indeed those of the Laughing Gull.

On 23 May we also noticed a Ring-billed Gull standing next to the nest while the Laughing Gull incubated. Whenever the Laughing Gull left the nest, the Ring-billed Gull attempted to incubate the eggs. Observation totaling 55 minutes during 23 and 25 May revealed that the Laughing Gull incubated nearly 85% of the time and the Ring-billed Gull 15%, incubation being almost continuous. Although Ring-billed Gulls at surrounding nests occasionally postured threateningly at the Laughing Gull, its partner in incubation showed no such aggression. On 4 June the nest contained a third egg, apparently contributed by the Ring-billed Gull. It was visibly larger than the other two and similar in size (55.6 × 39.7 mm) to the eggs of Ring-billed Gulls in nearby nests. Both birds continued to share incubation until 11 June, when the eggs disappeared. The Laughing Gull did not attempt to renest, but remained in the colony until at least 5 July.

To the best of our knowledge, this represents the first recorded nesting attempt by a Laughing Gull on the Great Lakes.

*Acknowledgment.*—The senior author wishes to thank the Charles A. Lindbergh Fund for generously supporting his research.—ELLIOT J. TRAMER, *Dept. Biology, Univ. Toledo, Toledo, Ohio 43606*; AND LOUIS W. CAMPBELL, *4531 Walker Ave., Toledo, Ohio 43612.* *Received 19 Apr. 1985, accepted 9 July 1985.*

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**Adult male Blue Grouse eats lizards.**—Although adult Blue Grouse (*Dendragapus obscurus*) primarily eat vegetation, they often include some animal matter in their diets (Beer, J. Wildl. Manage. 7:32–44, 1943; Stewart, Condor 46:112–120, 1944; Boag, J. Wildl. Manage. 27:555–562, 1963; King and Bendell, Can. J. Zool. 60:3268–3281, 1982). Spiders, centipedes, millipedes, snails, and especially insects (i.e., short-horned grasshoppers [Acrididae], froghoppers [Cercopidae], beetles [Coleoptera], and ants [Formicidae]) are eaten by Blue Grouse (Beer 1943; Boag 1963; King, Syesis 6:121–125, 1973; King and Bendell 1982). Here I report what is apparently the first record of Blue Grouse eating a vertebrate.

On 25 September 1982, one male and one female Blue Grouse were shot together on the southwest slope of Mount Shasta about 8 km north of McCloud, Siskiyou County, California (elevation = 1500 m). No other grouse were examined. The area consisted of second growth white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*), with *Arctostaphylos patula* and *Ceanothus velutinus* occurring in dense stands. Bittercherry (*Prunus emarginata*) was less dense.

The crop of the male grouse contained two recently born northern alligator lizards (*Gerrhonotus coeruleus*) with total lengths of 85 and 90 mm including intact tails, 32 grasshoppers (Acrididae), 43 ripe bittercherry fruits, 4 bittercherry leaves, 28 white fir needles, and grit. The crop of the female contained 8 grasshoppers, 166 ripe bittercherry fruits, and 1 bittercherry leaf.

Blue Grouse may actively select animal food, or ingest it accidentally (see King and Bendell 1982). In this report, ingestion of two lizards and many grasshoppers suggests that animals were selected. Blue Grouse select invertebrates that are often fairly large (Beer 1943). Newborn alligator lizards weigh about 1 g; the lizards reported here were not much larger than the grasshoppers consumed. Young lizards are abundant in northern forests for only a short

period in late summer and fall, and Blue Grouse probably rarely encounter lizards, or other vertebrates, sufficiently small enough to eat.

*Acknowledgments.*—I thank T. Simons and J. Prinz of McCloud for collecting the grouse and crop contents, and L. S. Simons and several reviewers for helpful comments.—Lee H. Simons, *Dept. Zoology, Arizona State Univ., Tempe, Arizona 85287.* *Received 2 Feb. 1985, accepted 23 July 1985.*

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# ORNITHOLOGICAL LITERATURE

AVIAN ECOLOGY. By C. M. Perrins and T. R. Birkhead. Methuen, Inc., 733 Third Avenue, New York, New York 10017, 1983:221 pp., 40 numbered tables, 76 numbered text figures, references, index. $21.00 (paper).— This book is designed to fill the authors' perceived gap in the literature of material for ". . . the advanced undergraduate and the serious amateur wishing to know more about the ways of birds . . . ." After a brief introduction there are eight chapters ranging in topic from social systems through reproduction and migration in which the authors attempt to tell us a little about each of the major topics in the ecology of birds. Owing to the geographic location of the authors, the book is decidedly slanted towards the European literature and for the most part ignores many of the "traditional" examples from North America. This is not necessarily a criticism, however, as I for one am really behind on the European literature and found this book to be quite informative in that regard.

In Chapter 1 the authors give an overview of their approach to the book in which they discuss each characteristic from its adaptive standpoint and compare the experimental and comparative approaches to bird biology. Chapter 2 deals with social systems, namely territoriality and coloniality. Territoriality, shown to be the result of competition for scarce resources, is said to limit populations. Brown's economic defendability model is supported with Gill and Wolf's fine sunbird study. Interspecific territoriality is examined using Reed's Great Tit (*Parus major*) and Chaffinch (*Fringilla coelebs*) study. The advantages of coloniality are divided into antipredator and feeding categories, while the costs are listed as increased competition, risks of rearing unrelated young, cannibalism, and increased transmission of ectoparasites and disease. As in the remaining chapters, Chapter 2 ends with a short summary.

Breeding systems are the subject of Chapter 3, which is basically a synopsis of Lack's, Orian's, and Emlen and Oring's papers. Short sections on brood parasitism and cooperative breeding are included (cf. Table 3.3 for a good summary of the costs and benefits of cooperative breeding). Reproductive biology is divided into two chapters: Chapter 4 on breeding seasons and Chapter 5 on clutch size. The general tone of the two chapters centers around the trade-off between the date at which birds start to breed and the number of eggs they lay. The review of proximate and ultimate factors at the start of Chapter 4 is refreshing. The discussion of clutch size quickly dismisses all theories other than Lack's idea ". . . that the clutch size that evolves is that which leads to the parents rearing the largest number of young which survive to breed." The strengths and weaknesses of the theory are discussed and recent modifications (e.g., Ricklefs, Charnov, and Krebs) to the parent idea are summarized.

Chapter 6 covers population biology, including the illusive concept of stability; rates of increase; carrying capacity and limiting resources; survival rates and life tables; natural regulation of population density (density-dependent and density-independent factors); and a catch-all section on practical applications with paragraphs on species protection, reduction of pest species, and exploitation (e.g., hunting). I feel the strength of this chapter is the synthesis of ideas on density-dependent and independent factors, while the weakness lies in the discussion of Wynne-Edward's old ideas on social regulation. Let the dead rest in peace.

Initially, my interest in the book was drawn to Chapter 7, bird communities. After a short overview of concepts, at a highly simplified level which might turn off people who have had one ecology course, the authors present a discussion of niche theory based on the premise that ". . . we are observing a situation as it is and trying to infer what caused it," a problem that all bird ecologists know to be nontrivial. Unfortunately, the authors do not present any

of their ideas to solve the problem, nor do they give an adequate survey of the relevant literature. The sections on resource partitioning and "evidence for competition" are too vague to be of much use as reference material and not insightful enough to be stimulating. The authors end this chapter with a short section on island biology but ignore the recent controversies regarding turnover rates, equilibrium theory, and island (refuge) size. In sum, I found this chapter to be somewhat disappointing.

In contrast, I found Chapter 8 on foraging behavior to be very interesting, again, however, at the simplified level. The chapter is based on the pros and cons of Charnov's optimal foraging model, including Cowies' laboratory test of the model using Great Tits and Krebs and Davies' famous conveyor belt study. A discussion of solitary versus group foraging is presented, and the chapter ends with a summary table of conclusions on the optimal foraging approach. The book finishes with a very short summary of the work done on migration, completely ignoring Cox's ideas on the role of competition in the evolution of migration.

My overall impression of the book is that it is probably good for advanced undergraduate students in European schools. Its suitability for North American schools is somewhat limited, however. For example, as none of the scientific names are given (a major fault in this book) the typical North American bird student, or amateur birder, is unlikely to know that a "Sand Martin" is a Bank Swallow (*Riparia riparia*). Moreover, although university libraries may have many of the European literature citations (e.g., Ibis, Nature, Ornis Scand.) it is unlikely that the "serious amateur" would have access to such literature and, therefore, follow-up work to that in the original text would be difficult to obtain.

Editorially the book is well done. Aside from a few minor errors (Bluebird [*Sialia* spp.] as two words and then as one in the same paragraph) the work is clear. I found all of a random sample of 30 text citations in the reference section. In sum, the text is not sufficiently detailed to be useful as a reference book, and it is too specific to be used in an ornithology class; however, as an intermediate between the two it hits the mark. I wonder if there is such a market in the U.S.?—ROBERT C. WHITMORE.

THE GROWTH AND DEVELOPMENT OF BIRDS. By Raymond J. O'Connor. John Wiley and Sons, New York, New York, 1984:315 pp., 96 numbered text figs., 45 tables. $39.95.—The contents of this book are much broader and of interest to a much wider audience than indicated by the title. The aim of the book appears to be to summarize current knowledge of all aspects of young birds, including physical and behavioral development from egg to experienced adult. A unifying theme is an emphasis on the selective advantage of physical and behavioral adaptations to the young bird's environment, including such aspects as nest location, food type, predation level, population density, and habitat stability. Differences resulting from the precocial-altricial spectrum are brought out well. In addition to thorough coverage of physical development, there are chapters on feeding, imprinting, instinct and learning, migration and dispersal, and song.

This broad coverage is both a strength and a weakness. The book should find its largest audience among students and others wanting an introduction to and review of the subjects discussed. It is immensely readable, and full of fascinating nuggets of information, from the number of tastebuds in a hatchling, to the ability of some birds to carry their young between their legs. Very scattered literature has been brought together, and classic studies are described in some detail, giving methods as well as results. Some indications are given of where further work is particularly needed, although it isn't always clear which chapters present everything known on a subject and which are a general introduction to a topic. Innumerable ideas for Ph.D. research came to mind as I read.

Readers already well-versed in certain fields of study in avian growth and development also will find this book interesting, though perhaps of less practical use. It is salutary to be reminded that one's own field of endeavor occasionally should be viewed in the wider context of a bird's entire developmental strategy, though it is hard to integrate, for example, development of nestling thermoregulation with song learning. Specialists will find nothing new in the chapters on their own areas, even though coverage seems very good.

The information was accurate for areas I know something about, although I disagreed occasionally with O'Connor's interpretations. In several places there is a tendency to equate correlation with cause and effect (e.g., on pp. 89 and 106). A homely cover, more than a few typographical errors, and O'Connor's predilection for exclamation marks are all small points that will irk some readers. This book is generally a good source of more specialized references (through about 1980), but I found several items I wanted to pursue (such as in Table 2.1) that were not accompanied by a citation. Some important ideas were excluded due to their recent publication (e.g., Clark and Wilson's views on hatch asynchrony, Quart. Rev. Biol. 56:253–277, 1981), but the book's broadness of coverage should help preclude the rapid obsolescence a more narrowly focused text might face.

I agree wholeheartedly with O'Connor ". . . that single factor explanations are inadequate, development patterns being most properly viewed as only one component in total life histories . . ." (p. 70). It was rather disappointing, therefore, that there was not more emphasis on and reiteration of this point; a final tie-up chapter would have been a welcome addition. However, the success of the book as a current overview of a very broad subject, previously unsummarized and burgeoning with new research, is undeniable. High readability and relatively low price make this book accessible to a wide audience, and it will prove a worthwhile read for people working with young birds in any capacity.—Erica H. Dunn.

Coastal Waders and Wildfowl in Winter. By P. R. Evans, J. D. Goss-Custard, and W. G. Hale (eds.). Cambridge Univ. Press, London, England, and New York, New York, 1984:331 pp., 115 numbered text figs., 32 tables. $54.00.—This hefty sum buys knowledge, clear thinking, and insight into the ecology and conservation of shorebirds and ducks in marine habitats. It also purchases substantial doses of speculation, curious logic, and even some aggravation.

The book emerges from a symposium held in Texel, the Netherlands, in 1981, sponsored by the Wader Study Group, an international body coordinating shorebird research. In the preface, the editors state their hope that students of animal ecology and behavior as well as ornithologists interested in the conservation of birds of coastal habitats, will find the book valuable. They shall, although I doubt so valuable that many individuals beyond a dedicated core of specialists will pay $0.16/page.

The book is divided into three sections with the editors taking separate responsibility for the contents of each part: food resources and energetics (Evans, 6 chapters), social behavior (Goss-Custard, 5 chapters), and overviews of geographic regions and their roles in the Palearctic-African migration system (Hale, 8 chapters). With a total of 19 chapters plus an introduction to each section, the 331 pages scatter into many short works. Too little space is available for this review to comment on them all.

The first chapter (Evans and Dugan) offers a sweeping overview of the relationship between shorebird predators and their invertebrate prey. Anyone contemplating ecological work in this field should read Evans and Dugan's chapter. Many avian ecologists labor under the impression that the shorebird-invertebrate system is simple and therefore easy to study. Relative to most other avian predator-prey systems, perhaps it is. But Evans and Dugan

lay level upon level of complexity onto the relationship. The simplicity of shorebird ecology is that its complexity is conspicuous, unavoidable, and dissectable. War is peace, etc.

Seven of the remaining 10 chapters in sections 1 and 2 focus on shorebirds; the other three on ducks. In all, they make good reading. For example, Pienkowski, Ferns, Davidson and Worral develop a logical structure for studying the foraging energetics of shorebirds while Townshend, Dugan, and Pienkowski set forth a fascinating natural history of Black-bellied Plover (*Pluvialis squatarola*) winter territoriality. Goss-Custard and le V. dit Durell coauthor a fine exploration of Eurasian Oystercatcher (*Haematopus ostralegus*) population dynamics. They show that density-dependence is far from being a dead issue, particularly in the behavioral mechanisms by which the dependence comes about. Their use of computer simulation is refreshingly appropriate and helpful.

Several Dutch workers offer powerful contributions. Zwarts and Wanink's chapter on clam predation by Eurasian Oystercatchers and Eurasian Curlews (*Numenius arquata*) drives home the complexity point (above) further. Their data on the large differences in reward between prey of similar sizes should produce sleepless nights for anyone whose study does not discriminate carefully among prey size classes.

Then from whence the aggravation? My chief complaint is the emphasis on weaving stories from patchy data. Facts are marshalled in favor of interpretations, rarely against. While I don't want to ride the hobbyhorse of hypothesis-testing, a healthier skepticism towards one's own ideas would have benefitted the execution of a number of these chapters. Readers should watch for unproven generalities offered as fact (e.g., Chapter 2: "Most waders regulate their weight in winter") and a selective use of literature. Despite new interest in theories on "action at a distance," I doubt that endless citations to one's own prior papers will improve the original results.

C. Swennen's chapter on roosting flocks of Eurasian Oystercatchers is simply excellent. Work such as this should have antedated all the speculative frenzy about roost adaptive function. His results show that the quality and health of individuals varies strongly among roosts, with important implications for theory, management, and research technique.

The final eight chapters, save one, describe various wader concentration areas in the Palearctic-African migration system. The sites included are done well, if briefly. Several interesting themes are developed, especially on prey biomass removed and correcting estimates by factoring in the turnover of individuals. Nothing is said about Spain, France, nor the Mediterranean. I would have preferred Hale's concluding chapter to be an overview of the individual contributions within this section, rather than what it is: Hale's unlikely arguments about the role of secondary hybridization in producing large races of shorebird and speculative scenarios of population changes in waders during the last 20,000 years.

Thus, as any multi-authored symposium volume in an active field, this book has passages of strength as well as weakness. It is never boring and the authors write clearly and incisively. Read it. Your time will be well spent.—J. P. Myers.

Experimental Behavioral Ecology and Sociobiology. By Bert Hölldobler and Martin Lindauer (eds.). Sinauer Associates, Sunderland, Massachusetts, 1985:xiv + 488 pp., text figs. $30.00 (paper), $55.00 (cloth).—I regret to report that the title is a con. This volume is not (as one might think) a potential competitor of Krebs and Davies nor even a general book about behavioral ecology and sociobiology. In fact, it is the proceedings of a symposium to the memory of Nobel Laureate Karl von Frisch, and most of the contributions are about bees. Indeed, the book prostrates any reasonable distinctiveness of behavioral ecology and sociobiology by defining them jointly as comprising "the study of the evolutionary adaptiveness of behavior in general" (p. 1), which I always took to be one aim of ethology. And

one finds Niko Tinbergen, who shared the 1973 Nobel Prize with von Frisch, called "the great experimental behavioral ecologist," whom I always took to be a founding father of ethology. Oh well, what's in a "buzz-word?"

There are five major sections: orientation, learning, and foraging (five papers on bees and ants); analysis of communication signals (two papers on bees, one more general, one on birds, one on primates); communication and reproductive behavior (three papers on hymenopterans, one a bit more general); social organization (four papers on social insects, one on birds, one on primates); physiology and societies (three papers on arthropods, one more general, one on tree shrews); and an epilogue about cognitive dimensions of communication. The chapters are infuriatingly unnumbered, and, therefore, not conveniently referred to, but among those unlikely to interest most ornithologists I especially enjoyed the contributions of Wehner and Rossel (on bee orientation), Michener (on the evolution of eusociality of bees), and Wilson (on the evolution of castes in ants). Many of the papers concern material already published elsewhere.

Chapters likely to interest readers of the Wilson Bulletin are few, as suggested by the above overview. Markl contributes a somewhat general chapter on communication illustrated mostly by insects, while Sherman and Holmes write on kin recognition, illustrating it with some avian material but concentrating on ground squirrels. Griffin's epilogue also mentions birds. There are, in the end, only two manifestly ornithological papers. That by Emlen and Vehrencamp on cooperative breeding was already published in an earlier version in "Perspectives in Ornithology" (Cambridge Univ. Press, New York, New York, 1983), whereas Scheich's chapter on auditory brain organization is new material. The former authors trace those environmental factors (habitat saturation and unpredictable ecological fluctuations) that promote helping to rear offspring of close kin as the best fitness strategy when reproduction is impossible. They also try, less successfully I believe, to account for differences in cooperative breeding, such as the extremes of helpers-at-the-nest and fully communal nesting.

Scheich presents some truly surprising findings based on a method of injecting 2-deoxyglucose labeled with carbon-14 into the blood. Those neurons of the auditory field L—the primary projection area of the telencephalon—were activated by a sound to take up the deoxyglucose and mark the brain cells for autoradiographic analysis. Studying the guinea fowl, Scheich and coworkers discovered that the brain responds not to the loudest frequency components in calls, but rather to the frequency having greatest contrast with other components. Furthermore, when a call is frequency-modulated there is a contrast-enhancement analyzing mechanism to process recognition. Scheich points out that the effects of attenuation and reverberation of calls in the natural environment need to be reanalyzed in terms of frequency-contrast and its enhancement if we are to understand properly ecological constraints on vocal communication.

There are some excellent papers in this volume, but my copy will not go on my sociobiology or ornithology shelves, but rather will take its place alongside von Frisch's various classics on bees.—JACK P. HAILMAN.

BIRD NAVIGATION: THE SOLUTION OF A MYSTERY? By R. Robin Baker. Holmes and Meier Publ., New York, New York, 1984:230 pp., numerous figs. and black-and-white photographs. $24.50 (paper), $32.50 (hard cover).—This book treats anyone interested in bird navigation to the whole realm of past and present research on the topic. For the serious student of migration or homing, it presents an excellent review of experiments, criticisms, and models of all of the main schools of thought on how birds navigate. The interested

layman, however, can be introduced to and captivated by the subject matter easily, as it is written in nontechnical language.

The reader is first given an historical review of the study of bird navigation from Aristotle to the work of the 1980s. Following a chapter on terminology and the definition of navigation, the major experimental techniques and tools are described. Then each of the major possible navigating cues is covered chapter by chapter. These include discussions of the use of landmarks, smell, an inborn compass, magnetic influence, stars, and grid maps. Each chapter offers not only summaries of many experiments, but discussions of the merits and flaws of the research.

The closing chapters present the reader with two hypothetical journeys. The currently accepted sensory cues used by birds are put into action, first by a homing pigeon returning to its loft and, second, for an hypothetical passerine on a long-distance migration. The last chapter looks at the future of navigation research.

The stated aims of the book are to present the facts and interpretations of the methods of navigation and to relate them to past theories as well as identify the main areas of future research. The author succeeds admirably with his interpretations, which repeatedly demonstrate the complexity of behavioral studies, particularly the problems of reproducibility and the near impossibility of eliminating all outside influences during experimentation. For example, he notes the presence of low frequency sound and distorted magnetic fields in a planetarium during experiments testing orientation to the rotation of an artificial sky compared to the rotation of the magnetic field. An artificial 50Hz noise is present in all modern buildings. In addition, the intensity of the magnetic field is lower inside a building. The author also points out that the very rotation of the magnetic field introduces another variation.

"Bird Navigation" is an excellent reference book for demonstrating the process of stimulation of ideas through controversy, the evolution of theories, and the use of the scientific method. Even the extensive list of references (20 pp.) is reason enough for the serious student of navigation to purchase this book.—ALLAN H. WERDEN.

A FIELD GUIDE TO BIRDS OF THE USSR. By V. E. Flint, R. L. Boehme, Y. V. Kostin, and A. A. Kuznetzov, translated by Natalia Burso-Leland. Princeton Univ. Press, Princeton, New Jersey, 1984:xxxi + 7 + 353 pp., 48 color plates (by Kostin), 303 maps, 71 text figs. $65.00.—The progenitor of this book had 635 pp., which were 3 cm shorter and one cm narrower than the U.S. Production. There was little front matter and usually two species per map. The 48 plates were together near the back. It was published by "Mysl" in Moscow in 1968, in an edition of 50,000—very large for a Russian ornithological work. The price was 2 rubles and 12 kopecs in hardcover. It has long been unavailable. This reflects the growing popular interest in U.S.S.R. birds.

The new book, in English ("American?"), includes a useful map of biotic zones (discussed in text), a brief discussion of birds in each zone, helpful hints for the bird-minded traveler, and other information. The problems of translating, updating and adding new material from Flint, and editing were considerable, and nitpickers have some ready-made opportunities. Pages are in two columns, set in smaller type than the original; the maps (some modified or updated) are of the same size as originally, and a few are confusing in detail (e.g., where three species overlap in distribution).

The color plates (same size in both printings) show the birds in static poses, all usually facing the same way (mostly to the left); originally, a few were in register, but most were slightly blurred. The American reproductions appear cleaner and inked more lightly; there is a definite reduction in richness of coloring. My preference is for the coloring of the original

reproductions, although the new printing is perfect in register and reveals that Kostin's "art work" is more precisely detailed than shown earlier. The plates are useful—all those pipits, shrikes, thrushes, wheatears, warblers, buntings, etc.!

Species accounts are assigned and indexed by consecutive numbers (not pages). The names in English, Latin, and Russian (transliterated) are given, as well as a plate number and map number. There are then sections on "Field Marks," "Habits," "Range and Distribution," and "Similar Species." Much is revised and expanded. An odd touch: food habits are mentioned in this field guide.

There is an index of English names and a cross-reference list (40 pp.) giving technical names in taxonomic sequence, variant names in English, plate, and map numbers. There is also an index of generic names and another of Russian vernaculars.

The user will have a few problems with this book. For example, Moryanka ["little sailor" in Russian] is bird (not page) no. 104, but in the English index is "Oldsquaw" (*Clangula hyemalis*) and numbered 711–712; these numbers are assigned correctly in the cross-reference list to orioles. There are a few quirks. For example, on the plates, the fulmar still stands high (like gulls) and two small petrels high also (like terns).

This may be the highest-priced guide to date. In North America, who will buy it? All ornitho-bibliomaniacs. Many libraries. A novice birder who can afford a USSR visit may want it; but, east as far as the Urals, a visitor is likely to feel comfortable (as do some Russians) with one of the more portable European guides (plus an escort who knows some birds and where they are). The hard-core "lister" already will know more birds than practically any Russian tour leader and probably will debate with his companions some taxonomic treatments in this book (*Sitta* complex, for example)—am I, or am I not, adding a species to my life list?

The intrepid peripatetic birder will supplement this new USSR guide with Colin Harrison's western palearctic *Atlas* (Princeton Univ. Press, Princeton, New Jersey, 1982), in part because many of its attractive maps cover far more geography to the eastward than the book's title. Also eastward and overlapping is Meyer de Schauensee's *The Birds of China* (Smithsonian Inst. Press, Washington, D.C., 1984), of same overall size but thicker, with 38 color plates. None of the three is down to proper field guide size. Stacked (all in hardcover), they measure 25 × 17.5 cm by 9.5 cm high, weigh 2.76 kg (6 lb), and cost $135.00. After a hard (?) day's birding, a little vodka along with comparing passages in these books should round out many an evening.—Ralph S. Palmer.

Roberts' Birds of Southern Africa, 5th Edition. By Gordon Lindsay Maclean, illus. by Kenneth Newman and Geoff Lockwood. Trustees of the John Voelcker Bird Book Fund, Cape Town, South Africa, 1985:848 pp., 76 color plates. No price given.—Austin Roberts's Birds of South Africa was first published in 1940 and underwent three editions by G. R. McLachlan and R. Liversidge. Only a few years after "Roberts 4th" was published (1978), Maclean has written a new edition, with mostly new illustrations and a rewritten text. The book covers the region south of the Caprivi and Zambezi River. Many changes in names, both common and scientific, are seen. The common names are based on a survey of 100 ornithologists, and the author justifies the South African bias against names used elsewhere (such as in Zimbabwe) on a one man-one vote criterion: the 100 were mainly from South Africa, and there are more English-speaking ornithologists there than in East Africa, even counting the tourists, says Maclean. By this criterion the names will not be acceptable to world birders.

The most significant improvement in Roberts 5th is the color plates. Newman's plates in Roberts 4th were poorly printed; they are more true to color and sharp in the present edition. Lockwood's plates are good too, but in many the colors are dull (at least in my copy). The

last two color plates range from albatrosses through finches, species reported within the area only in the past few years; these are done on a scale incompatible with the corresponding similar species on the other plates.

The text is well organized in species accounts, nearly a page per species (887 species are recognized), each with measurements, identification, distribution, habits, food, voice, and breeding. Measurements (wing, bill, weight, etc.) are taken where available from the original Roberts (1940) or from other sources, not acknowledged in the text, and not all are from populations in southern Africa. In some species the sexes were measured separately, in some they were not. The sketches of wing and feather shapes in Roberts 4th have been deleted; they will be missed by banders and museum workers who try to identify certain *Cisticola* warblers, *Lamprotornis* glossy starlings, and *Lagonosticta* firefinches.

Range maps within southern Africa are in green, yellow, or blue (resident, breeding, or nonbreeding); few have more than one color. The distributions are generally like those in Roberts 4th. The yellow spots in these maps are nearly invisible. Where ranges have changed (e.g., the Grey-headed Sparrow (*Passer griseus*) southwest through much of the Cape Province), no reason is given, nor is the extension mentioned. No overall detailed map with most place names mentioned is given, nor is there a gazetteer.

"Voice" sections include sonagrams for more than half of the species. These are useful for birds with only one common call, and the sonagrams often convey the differences among visiting wader species better than the words given to the calls. They are less useful in birds with regional or individual differences or those with large repertoires (as in the firefinches (*Lagonosticta rubricata* and *L. rhodopareia*), and still less when the figure shows the alarm call and not the song (*L. senegala, L. rufopicta* = "*L. nitidula*").

"Breeding" sections include seasons, clutch size, nest description, egg descriptions, and comments on incubation and nestling periods. For those species with which I am most familiar, misinformation is scarce. There is no evidence to conclude as does the author that a female Village Indigobird (*Vidua chalybeata*) lays only one egg in a particular nest of its foster species; in aviary observations individuals lay more than one in a nest. Successful brood parasitism by the Pin-tailed Whydah (*V. macroura*) is limited to *Estrilda* waxbird species, and certainly does not occur in *Cisticola* and *Prinia* warblers. Fewer than half of the species have one or more recent references; in most cases these are in recent issues of Ostrich or Bokmakierie.

What has been lost in this edition is the perspective of geographic variation among populations and of the history of ornithology in Africa. Authorship and type locality were excluded for the species, and with very few exceptions subspecies names do not appear. One consequence is that birders in different parts of the region may misidentify species that varied geographically in color. For example *Vidua chalybeata* populations in the Okavango-Cunene area have a white, not red, bill, and this species is, in fact, the only common indigobird known in this area. By ignoring subspecies and the notion of geographic variation, the author mistakenly "gives" the area to other species of white-billed indigobirds, one (*V. funerea*) whose foster species (*L. rubricata*) is unknown within hundreds of km (as is the indigobird); the other ("*V. incognita*" = *V. wilsoni*), was described from aviary birds imported possibly from Zaire and is unknown in the field anywhere in Africa, though its foster species *L. rufopicta* (=*L. nitidula*) does occur within the region. Including such records on the basis of identifications that were made without knowledge of the variation within and among species in the present work can only confuse our ornithological science. In a few other cases, a vestige of information in the earlier infraspecific taxonomy is seen where subspecies have been split into "species." Problematic "new" species that usually have been considered races of more widespread species include the Ashy Tit (*Parus cinerascens* = *P. afer cinerascens*) and the Mountain Pipit (*Anthus hoeschi* ? = *A. cameroonensis*) (usually

included in *A. novaeseelandiae*). No breeding sympatry is known between the forms, nor are differences in display behavior, so we have no strong reason to infer more than one species. At least questions such as these could be asked if a brief list of subspecies accounts and traits were available, as in the earlier volumes. Any list of subspecies is potentially a set of hypotheses about species limits, and can be tested in the field in possible areas of contact, but today's reader of Roberts' 5th will not have these when he goes into the field, and so the questions in systematics may not even be asked.

Roberts 5th summarizes a wealth of field data on the bird species and shows southern Africa to be a relatively well studied avifauna. This is the best book available on identification and biology of the birds of southern Africa, and it is one of the outstanding regional ornithology guides of the world.—ROBERT B. PAYNE.

SOUTH AFRICAN RED DATA BOOK—BIRDS. By R. K. Brooke. South African National Scientific Programmes Report No. 97, Foundation for Research Development, Council for Scientific and Industrial Research, P.O. Box 395, Pretoria 0001, South Africa, 1984:vii + 213 pp., no price given (paper).—The rare and endangered species of birds of South Africa were inventoried previously in "The South African Red Data Book—Aves," by W. R. Siegfried et al. in this series in 1976. The present book is both an inventory and a conservation analysis of the same avifauna. The objectives were to (1) establish which locally breeding species are rare or threatened enough to warrant formal recognition or action, (2) define the rarity of and threats to each species, (3) determine conservation priorities, and (4) determine priorities for research. General comparisons by habitat are summarized, and a series of categories is used to assess the degree to which each species is threatened and deserves action.

The region as defined includes South Africa, Lesotho, and Swaziland. Within South Africa, the national states or homelands, as well as the four provinces, have their own conservation ordinances.

The text is organized into species accounts with detailed range maps of present and former distributions; summaries of habitat, status, estimated numbers and population trends; breeding rate in the wild (clutch-size, number of broods, incubation period, age at which females first breed), reasons for population changes; numbers known in captivity and the prognosis for captive breeding; current research efforts; the distribution and numbers in other parts of the species range; and references. The bibliography includes more than 1000 references and is up-to-date. The 1976 Red Book was useful to research workers; the author lists the published papers and theses in which it was cited and more than half of the species were cited therein.

Of the 108 species regarded as rare, threatened, or endangered in the book, six are birds of the Southern Ocean. Of the 102 mainland breeding species, 49 (48%) are associated with grasslands and wetlands; a recommendation that the biomes most in need of ecological study and conservation are the grasslands, marshes, and estuaries may guide further efforts. Several larks are endemic to South Africa, and their distributional ranges have contracted drastically over the past decades (particularly in the northern Cape Province, East Griqualand, and the Orange Free State) due to habitat changes associated with agriculture and domestic stock. Changes in abundance and distribution within the past 10 years are less evident; more of the differences evident in the species in this book and its 1976 predecessor are due to changes in the criteria used to recognize rare and endangered species than to changes in habitat or success in conservation efforts.

The five species with the highest recommended priority for conservation action indicate the historical and ecological factors involved as well as the strongly regional emphasis of the book. The Blue Swallow (*Hirundo atrocaerulea*) breeds locally in several counties of

southern and eastern Africa but is given the highest priority. Its high priority derives in part from an erroneously scored regional uniqueness ("all of the population in southern Africa" in the priority table) and, in part, from a population decrease in this century (it nests underground on grassy hillsides in high rainfall areas, now often planted with commercial crops and unsuitable for nesting; overgrazing and flash floods also result in unsuitable habitats). In contrast, Maclean (Roberts' Birds of Southern Africa, 5th ed., 1985, see above review) gives the status as "Uncommon to rare . . . but not immediately threatened; at most 5–6 pairs/km$^2$." Egyptian Vultures (*Neophron percnopterus*), with a population widespread in nonforested parts of Africa, southwestern Asia, and the Indian peninsula, are known as breeding birds in South Africa only from one old record in the Transkei. Historical decrease of the species in South Africa is due to poisoned carcasses and to attacks by farmers for the vulture's feeding on Ostrich (*Struthio camelus*) eggs and chicks. Perhaps also the feeding ecology has changed with the destruction of herds of antelope. Jackass Penguins (*Spheniscus demersus*) are endemic and have decreased in numbers due to intense commercial cropping of eggs well into the 1960s. Commercial exploitation of surface-shoaling fish near the colonies, oil pollution of the sea, and the continuing destruction of the colony habitat by commercial guano harvesting continue to depress penguin numbers, currently estimated at between 50,000 and 170,000 pairs. Yellow-billed Oxpeckers (*Buphagus africanus*) are widespread elsewhere in Africa but are rare and have not bred in South Africa since 1910, due to game decimation, cattle disease, and arsenic pollution of cattle. Roseate Terns (*Sterna dougallii*) are restricted as breeding birds in South Africa to one coastal site, but have a wide breeding distribution in the northern hemisphere.

The emphasis is clearly on those species that are rare within South Africa with less material on the South African endemics. The book is a useful source of information about the biology and conservation of the included species of southern Africa birds.—ROBERT B. PAYNE.

TUNNICLIFFE'S BIRDS, MEASURED DRAWINGS. By C. F. Tunnicliffe RA, introduction and commentary by Noel F. Cusa. Little, Brown, and Company, Boston, Massachusetts, 1984: 160 pp., 80 color plates, most with commentary. $49.95.—"Charles F. Tunnicliffe was born and raised on a farm near Macclesfield, England in the early years of this century. He studied at the Royal College of Art and took up etching and engraving in the 1920s. In 1932 he illustrated Tarka the Otter for Henry Williamson and began a long and prolific career as a wood engraver and book illustrator. His fascination with birds developed during the prewar years. In 1947 he left Macclesfield to live in Anglesey, where he spent the rest of his life. An indefatigable worker, he eventually became a popular watercolorist specializing in natural history subjects." This quote from the back of the dust jacket gives an insight into Tunnicliffe the man, but looking at his work gives the best insight into his love of and sensitivity to birds. His measured drawings are exactly as the name implies. Each bird is drawn life-sized, in a variety of poses, on a single Imperial sheet of paper. The drawings are made from fresh (and, occasionally, not so fresh), unprepared birds, that are meticulously measured with calipers. Occasionally very large birds occupy more than a single sheet of paper. Often scattered among the life-sized drawings are small sketches and vignettes to show particular feathers, other, usually nonsilhouetted, views of a head, the details of certain feather groups, or any details that Tunnicliffe wished to emphasize or include. Tunnicliffe's fine art training is not lost in his extremely detailed and accurate reproduction of the birds that he was drawing and painting. The arrangement of the pieces on each page makes for an incredibly beautiful work.

Tunnicliffe began making his measured drawings merely as references to be used in later paintings, but in his latter years he seemed to turn his attention more to the measured works. It was well known that he wanted people to save birds for him, and dead birds regularly appeared on his doorstep or in his mailbox, often with no indication of their source. It

seems that Tunnicliffe did not personally collect birds for his paintings, but he did let "everyone" know that anything they found dead was wanted. He also kept in contact with friends that hunted as well as with local game keepers (sadly, the lovely Golden Pheasant [*Chrysolophus pictus*] printed on the cover is not included in the book!). In his lifetime he produced about 300 of the measured drawings. The ones reproduced in the book were chosen to be representative.

There are four sections of paintings: "Predatory Birds," "Water Fowl," "Sea & Shore Birds" and "Miscellaneous Birds." The last section of the book is devoted to a memoir of Tunnicliffe by Noel Cusa.

This volume is a picture book, but a picture book full of life. Having kept many live birds and having prepared bird specimens, as well as being a painter of birds, I find myself wanting to look at the works over and over again. They are exquisite. The Tawny Owl (*Strix aluco*) on p. 37 looks as soft as I know it is; it has the right wing spread and I can "feel" the bones in it, and I find myself mentally flexing the legs, watching the talons and feet curl as the foot is drawn close to the body! The detailed drawing of the left half of the tail of a female [Green-winged] teal (*Anas crecca*) on p. 51 shows the blunt, whitish tips of extremely fresh fall plumage, and the dense, short plumage of a duck, so totally different from the plumage of the Tawny Owl. He often uses a colored background, working whites onto the paper with chalk or gouache. Two different [common] Black-headed Gulls (*Larus ridibundus*) on pp. 94 and 95, show how effectively the background color of the paper can be used to create the effects of cold and warm light on the subject. Tunnicliffe often and successfully shows head-on views of birds. A Little Auk (*Plautus alle*) (i.e., Dovekie [*Alle alle*]) on p. 101, a Whimbrel (*Numenius phaeopus*) on p. 111, and a [Eurasian] Jay (*Garrulus glandarius*) on p. 127, all illustrate his ability to show this difficult position. Furthermore, the Jay shows Tunnicliffe's sensitivity to the positions and changes of feather tracts, as well as the details of the rippling texture along the inner webs of the bird's secondaries. Artists who do not have close familiarity with live or fresh birds may be amazed to see how large and puffy the head on the Blue Tit (*Parus caeruleus*) on p. 145 appears, or how "dumpy" and short-tailed the Stonechat (*Saxicola torquata*) on p. 147 is.

Tunnicliffe used whatever he needed to get the effect he wanted, but he tended to work in a transparent manner—even when using an opaque medium such as gouache. This manner of working leaves his birds "fresh and fluffy," not hard and overworked. It is hard to give an impression of someone's work without making a comparison. I would have to say that Tunnicliffe's work reminds me of that of three artists—Louis Agassiz Fuertes, Lars Jonsson, and Larry McQueen.

The book is beautiful and anyone interested in looking at beautiful reference paintings of birds will want to own it. I strongly recommend the book also to anyone who paints or draws birds. The information contained in Tunnicliffe's work is extremely valuable, and also very inspirational. The fact that all of the birds are Old World, most being British, in no way detracts from the book's value and interest to anyone, anywhere in the world. The information about the birds and recollections of Tunnicliffe by Noel Cusa make an interesting contribution to the book, but it is the artwork that "steals the show." This is a "coffee table" book that deserves to be enjoyed, studied, and appreciated. I, for one, would like to see another volume produced. The binding, general construction, printing, and color work all seem to be very well done. The price is a bit high, but in 1985 that's the way it is!—JOHN P. O'NEILL.

HUMMINGBIRDS: THEIR LIFE AND BEHAVIOR. By Esther Q. Tyrrell, with photographs by Robert A. Tyrrell. Crown Publ., New York, New York, 1985:212 pp., 214 photographs, 26 drawings. $35.00.—This elegant book is in the finest tradition of coffee table books. Often there are several photographs per page, and relatively few pages have no photographs. The

book clearly is meant as a vehicle for the outstanding photographs of North American hummingbirds and many of the flowers they visit. The text is aimed at a lay audience and is modern in its treatment of hummingbird biology. Topics covered in the text include anatomy, feathers, flight, courtship and nesting, food and metabolism, behavior, and pollination. In addition, there is a list of plant species in North America visited by hummingbirds, a list of all species of hummingbirds, and a bibliography that includes many recent references. An early section of the book summarizes salient features of the biology of North American species of hummingbirds, with each species account accompanied by two photographs of the male, one showing a ventral and the other a dorsal view. A line drawing of the female, while well done, is not useful for identification, or for size comparisons.

The photographs, limited to species found in North America, illustrate points made in the text. For example, the section on feathers has some interesting pictures of hummingbirds in molt. Other photographs show torpid hummingbirds (birds with lowered body temperatures), birds cleaning their bills, and even with the long tongue extended well beyond the bill tip. What could have become a somewhat repetitious series of photographs of a limited number of species has been turned into an educational message in itself. The captions for the photographs clearly relate the picture to the textual material. In a few cases (e.g., p. 97) the caption is contrived to make the photographs illustrate the text.

A chapter on the techniques used to obtain the photographs would have been very informative. The text hints at the electronics necessary for these exceptionally detailed photographs, but a discussion of the time and effort involved in photographing these birds might have been very interesting to readers.

The text is easy to read and generally is free of errors. The author has read much of the modern and historical literature about hummingbirds and nicely juxtaposes early statements based on little or no direct observation with modern theories and research findings. Much of the discussion points out how hummingbirds differ from other birds in their biological characteristics, but in a few cases, such as parts of the discussion of anatomy, sections with little distinctive significance for hummingbirds are included for completeness. The use of jargon purposely is kept to a minimum, but a few terms are used that are not clearly defined. Occasional lapses occur in the metabolism section. Energy use is sometimes given as oxygen consumed without mention of conversion factors to calories. Torpor is mentioned without a definition until several pages later. A more interesting problem occurs when energetics are discussed in terms of calories. The small size of hummingbirds means that most people studying metabolism use the unit of the calorie, which is only 1/1000th of the Calorie normally referred to in human diets. The distinction is especially important when scaling metabolic rates of the birds and humans (p. 134). A similar interesting problem with units occurs on p. 56 when the text says hummingbirds may eat from 3 to 7 g of nectar from a feeder at one feeding. This amount, which would approximately equal the weight of these birds, is overstated by a factor of about 100. A few minor errors occur in the accounts of individual species: the Anna's Hummingbird (*Calypte anna*) now breeds fairly regularly in Arizona and the range of the Magnificent Hummingbird (*Eugenes fulgens*) extends to Costa Rica and Panama. However, is spite of these few minor mistakes, the author has done a very good job of making the biology of these unique birds accessible to the lay reader.

As with any book of this sort that attempts to cover so much material with minimal text, one can always mention items of interest that do not appear. Perhaps a diagram of the circulatory system would have helped the anatomy chapter. Some mention should have been made that the view of the figure of the reproductive tracts is from the ventral surface. This is not crucial for the male, but the female drawing has the ovary on the right side, while the text correctly states that the right ovary atrophies early in development. I think most lay readers would have benefited from more emphasis on the relatively small pro-

portion of a day that the birds spend flying. Most casual observers see hummingbirds at flowers and generally think they must spend most of the day flying.

The list of flowers pollinated by hummingbirds is taken from Johnsgard's recent book (*The Hummingbirds of North America*) and perpetuates the idea that visits by hummingbirds generally produce pollination. While that notion is correct in most cases, a sentence or two to indicate just how little is known about actual pollinators for many North American wildflowers might have been useful. The list of hummingbirds of the world seems an unnecessary addition as no information is given about ranges, merely a list of the common and scientific names.

While I feel that it is a reviewer's duty to point out errors and make suggestions for improvement, I want to emphasize that this is a first-rate book for its intended audience. It will not replace Crawford Greenewalt's equally striking book "Hummingbirds" (Doubleday, Garden City, New York, 1960) for those interested in photographs of more than North American species, but the diversity of photographs and their use in illustrating aspects of hummingbird biology make this an outstanding achievement.—LARRY L. WOLF.

BOBWHITE THESAURUS. By Thomas C. Scott. International Quail Foundation, Edgefield, South Carolina, 1985:306 pp. $29.95.—This may be the most useful book ever written for the Northern Bobwhite (*Colinus virginianus*) researcher. The thesaurus contains two sections: an index of subject-categories and the associated bibliography. Nearly 3000 publications have been indexed into 73 principal subject-categories. Listings in the subject-categories include geographic locations (often down to county level), when they are relevant to the findings. Time period involved also is included in the article listing when it is important to interpretation of data presented. The bibliography section includes all known publications prior to 1983 and covers over 100 years of bobwhite research.

Any person initiating a research project on the Northern Bobwhite will save considerable time, effort, and money by using this book. They will be assured of locating every article ever published on this species. Articles are not abstracted but the key words used in subject-categories enable researchers to select those specific articles that are relevant to their interest and geographic location.

Similar books for other species that have been the subject of extensive research will certainly be published as a result of the success of this one. Dr. Scott and The International Quail Foundation, which funded publication, have provided an invaluable service to bobwhite researchers and are to be commended for their efforts. The book is neatly and attractively done and is highly recommended.—EDWIN D. MICHAEL.

VOICES OF THE NEW WORLD JAYS, CROWS, AND THEIR ALLIES, FAMILY CORVIDAE. By John William Hardy (compiler and ed.). ARA9, ARA Records, Gainesville, Florida, 1984.—The jays as a group are notable for the complexity of their vocal behavior. To attempt to present recordings of all of the many and complex vocalizations of the New World corvids is a monumental task, and one at which Hardy has had considerable success. This record contains some recordings of all but one of the New World species. As a contributor to the record, I can find some very minor points to criticize about his handling of the Pinon Jay (*Gymnorhinus cyanocephalus*), but the criticisms are only of significance to one extremely familiar with that particular species. Overall, I find the recordings to be of very good quality and, for the species with which I am familiar, a fairly complete record of most vocalizations. The weak points of the record come almost totally from thc lack of good recordings of some calls of some species. What is here is good. What is not here is probably not available anywhere. I highly recommend the record as an excellent introduction to corvid vocalizations

to anyone who is contemplating work with jay vocalizations, or who is just interested in bird calls. I hope that Hardy will update the record 10 years from now as new recordings become available.—PATRICK D. MCARTHUR.

MODERN FALCONRY. By Jack Samson. Stackpole Books, Harrisburg, Pennsylvania, 1984: 160 pp., 42 photos, 19 line drawings. $12.95 (paper).—This is an attempt by the former editor and current editor-at-large of Field and Stream, Jack Samson, to provide a primer for beginning falconers who want to acquire a hawk or falcon and train, care, and equip them for hunting or recreational sport. Samson has drawn on his experience as head of the raptor division at the American Museum of Natural History's Trailside Museum in New York in the writing of this book. Considering Samson's stated professional accomplishments, the book adds little to the already large list of books or primers for beginning falconers. Many European books are available for a few dollars more, should one care to be exposed to this practice.

The book is divided into 21 chapters with such titles as: "How to Get Your Hawk"; "Flying to Fist and Lure—Kestrel/Sparrow Hawk"; "Releasing a Hawk to the Wild"; "Care and Treatment of Hawks"; "New Federal Falconry Regulations"; "Fact Sheet, Federal/State Qualifying Examination for Falconry Permit"; and "Whither Falconry?" Considering the subject matter to be found in other falconry books, the chapters on regulations and examinations may be the major contribution of the book. There is not a lot of professionalism evident considering the content. One chapter, for example, which deals with the "Sparrow Hawk" (*Falco sparverius*), is followed by a chapter on the Kestrel/Sparrow Hawk, with no clear indication that this is the same species referred to in the preceding chapter. Samson should have followed one terminology or the other throughout the book.

Some chapters are very informative, such as "How to Get Your Hawk," which is more or less cook-book in stylc, although without a lot of detail on how, for example, to tie a noose for a trap; other chapters are more-or-less bits of rambling information. An example of the latter is chapter 10 on the "Training and Flying the Merlin/Pigeon Hawk." Most of the four pages in the chapter are taken up by two photos; one is of a person with a lure and has nothing to do with the Merlin (*Falco columbarius*). Furthermore, the text deals more with biology of the species and the author's experience watching one hunt.

The photos vary from poor to good quality. The best photo is on the cover, which depicts an absolutely beautiful falcon that appears to be either a very dark Aleutian Peregine (*Falco peregrinus pealei*) or a hybrid peregrine (*F. p. pealei*) crossed with a dark Gyrfalcon (*F. rusticolus*). The chapter on the Prairie Falcon (*Falco mexicanus*) has a head photo (p. 98) of a Kestrel that is labeled as a Prairie Falcon.

Throughout, the book is relatively free of typographical errors, follows the general theme of conservation, and provides some new information, but overall, it adds little to one's library.—CLAYTON M. WHITE.

APPLIED STATISTICS AND THE SAS PROGRAMMING LANGUAGE. By Ronald P. Cody and Jeffrey K. Smith. North-Holland, New York, New York, 1985:187 pp., numerous figs. $14.95.—A substantial, perhaps overwhelming, number of ornithologists are now using computer software (SAS, SPSS, etc., for mainframe and minicomputers; ASYST, STAT/PROTRAN, etc., for microcomputers) to prepare their descriptive and inferential statistics. Although these programs provide an efficient, and at times essential, way of analyzing data, their accompanying documentation (user's guides, etc.) are sometimes perceived as unsurmountable barriers to the use of these programs. As a result, many ornithological data receive less-sophisticated treatment on handheld calculators, or they wind up being analyzed by a second party in the "Statistics Lab." "Applied Statistics and the SAS Programming Lan-

guage" is one of a recent cornucopia of books designed to hurtle would-be computer users over, or at least into, the documentation prepared by software publishers. In this instance the documentation in question is that prepared by the publishers of SAS (Statistical Analysis System) (SAS Institute Inc., Cary, North Carolina), one of the major statistical software packages. The usefulness of texts of this genre, and the reviewed text is no exception, depends upon the reader. The book is an unnecessary acquisition for those of us who have used SAS for some time and are accustomed to its documentation: there is little in this publication that we do not already know. And, unfortunately, the book will be of little use to that declining number of ornithologists who persist in acting like conscientious objectors to the computer age. The book will be useful, however, to those who are ready, willing, and eager to learn the whys and wherefores of statistical software (i.e., graduate students contemplating a less than rosy job market). The book also may be helpful to those who use SAS on an intermittent basis, and need a refresher course from time to time. This is not to say that the book is a substitute for the SAS publications "Introductory Guide," "SAS User's Guide: Basics," and "SAS User's Guide: Statistics." This volume is far too brief for that. But it does offer a second view and, for those who might be frightened off by the bulk of the SAS publications, Cody and Smith should help demystify the increasingly essential research tool that is computerized statistics.—K. L. B.

THE ATLAS OF BREEDING BIRDS OF VERMONT. By Sarah B. Laughlin and Douglas P. Kibbe (eds.). University Press of New England, Hanover, New Hampshire, 1985:456 pp., 12 maps, 199 line drawings and range maps, 8 transparent map overlays. $45.00.—Preparing atlases has become an increasingly popular endeavor among serious amateur birders throughout the East. Most of the eastern states have such projects at various stages of completion, but to Vermont goes the honor of being the first state to complete the project and publish the results.

For the possibly uninitiated, an atlas project is carried out by laying off a grid on the area being studied. Most eastern states have adopted the grid formed by the U.S.G.S. 7.5-minute quadrangle topographic maps (western states have usually adopted the latilong as a grid). Each grid block usually is divided into six blocks, each covering about 25 $km^2$. The aim is to establish a list of breeding birds for each of these blocks. Most atlases set up a graded series of criteria to classify a species, as a "Possible," "Probable," or "Confirmed" breeder. With the results obtained over what is usually a 5-year period, it then becomes possible to draw a fairly accurate map of the breeding range of a species in the state (or other political subdivision being studied).

The number of available birders in Vermont was small enough that the project leaders elected to cover only one randomly selected block in each quadrangle, and then to add a few others of special or unusual habitats. A total of 178 species was confirmed as breeding in the state, and 14 additional species were listed as either Possible or Probable. For each of the species there is a small pen-and-ink sketch of the bird, a page of text about the species, and map of the state indicating the blocks in which the species was recorded. A short table describes the distribution of the breeding blocks in the seven physiographic regions of the state. There is a set of eight plastic map overlays, making it possible to compare the breeding distribution of the species with such things as the Physiographic Regions, Vegetation Regions, etc. Accordingly, we have at hand a fine picture of the distribution of the breeding avifauna of Vermont in the late 1970s (working period was 1977 to 1981). This can serve as a baseline for future studies as changes occur.

The most unfortunate limitation on works such as these is that no attempts can be made to census the various species. The forests of Vermont contain many of the Neotropical migrants whose populations are thought to be declining. For example, the Ovenbird (*Seiurus*

*aurocapillus*) was found in 98% of the blocks surveyed, but we have no indication of the numbers involved. A block with a confirmed breeding record of one pair is indistinguishable from a block with 50 pairs. Elsewhere in its breeding range the species has declined greatly. A more or less subjective statement in the Ovenbird account says that the population "apparently" has not changed significantly over the last 100 years. I sincerely doubt that that statement can be true. I hope that as the various Atlas Projects come to completion some of the manpower used can be turned to the important task of making quantitative censuses of those species that are not adequately monitored by the Breeding Bird survey, which works best for roadside and edge species. Vermonters are to be congratulated for completing this project in such fine shape. The high percentage of Confirmed breeders speaks to the dedication and tenacity of the observers, as many of these species nest in areas of difficult terrain or forest cover. The publication is a most attractive one although its price may be prohibitive to some. A part of the text deals specifically with Vermont data, often giving migration dates and, in a few cases, populations. Apparently, the editors and project leaders wanted this volume to serve also as a one-volume "bird book" for the people of the state, as there is much general discussion of the birds' habits, habitat, and breeding biology that comes from other, readily available, sources and might well have been omitted.

We can look forward to additions to the Atlas of North American Breeding Birds as the various state projects come to completion, and we can hope that future state atlases are as successful as this one.—George A. Hall.

Birds of Nahanni National Park, Northwest Territories. By George W. Scotter, Wayne P. Neil, and J. David Henry. Special Publication No. 15, Saskatchewan Natural History Society, Box 1121, Regina, Saskatchewan, 1985:74 pp, 1 map, 13 black-and-white photographs and drawings. $7.00 (Canadian).—This attractive booklet, in the tradition of National Park booklets, both Canadian and U.S., lists brief annotations for 170 species known from this Park, which is located at about 61°N. The known breeding ranges of 10 species are extended and the Wandering Tattler (*Heteroscelus incanus*), Barred Owl (*Strix varia*), Hammond's Flycatcher (*Empidonax hammondii*), Clark's Nutcracker (*Nucifraga columbiana*), Philadelphia Vireo (*Vireo philadelphicus*), Black-throated Green Warbler (*Dendroica virens*), and Mourning Warbler (*Oporornis philadelphia*) are reported from the Northwest Territories for the first time.—George A. Hall.

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## The Wilson Bulletin

*Editor* Keith L. Bildstein
Department of Biology
Winthrop College
Rock Hill
South Carolina 29733

*Associate Editors* Michael W. Collopy
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*Review Editor* George A. Hall
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*Color Plate Editor* William A. Lunk
865 North Wagner
Road
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*Index Editor* Kathy G. Beal
Department of Biology
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Columbus, OH 43209


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See Wilson Bulletin, 97:606–607, 1985 for more detailed "Information for Authors."

Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts of major papers should be brief but quotable. In both Major Papers and General Notes, where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (AIBS, 1983). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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Membership inquiries should he sent to Dr. Richard Stiehl, Department of Biology, Southeast Missouri State Univ., Cape Girardeau, Missouri 63701.

## CONTENTS

*OTUS PETERSONI*, A NEW SCREECH-OWL FROM THE EASTERN ANDES, WITH SYSTEMATIC NOTES ON *O. COLOMBIANUS* AND *O. INGENS* ..... *John W. Fitzpatrick and John P. O'Neill* 1

MATING SYSTEM AND REPRODUCTIVE SUCCESS OF A SMALL POPULATION OF POLYGAMOUS SNOWY PLOVERS ..... *John S. Warriner, Jane C. Warriner, Gary W. Page, and Lynne E. Stenzel* 15

TEMPORAL DYNAMICS OF NEOTROPICAL BIRDS WITH SPECIAL REFERENCE TO FRUGIVORES IN SECOND-GROWTH WOODS ..... *Thomas E. Martin and James R. Karr* 38

STRUCTURE, SEASONAL DYNAMICS, AND HABITAT RELATIONSHIPS OF AVIAN COMMUNITIES IN SMALL EVEN-AGED FOREST STANDS ..... *Richard H. Yahner* 61

LATE SUMMER–SPRING MOVEMENTS OF JUVENILE SAGE GROUSE *Peter O. Dunn and Clait E. Braun* 83

ASSORTATIVE MATING AND SEXUAL DIMORPHISM IN THE COMMON TERN ... *Malcolm C. Coulter* 93

RUDDY TURNSTONES, GREAT HORNED OWLS, AND EGG LOSS FROM COMMON TERN CLUTCHES *Ralph D. Morris and David A. Wiggins* 101

PREY-SIZE SELECTION IN NESTING MALE AND FEMALE COOPER'S HAWKS *Patricia L. Kennedy and Donald R. Johnson* 110

HUNTING SUCCESS OF SOME MISSOURI RAPTORS ..... *Brian Toland* 116

GENERAL NOTES

- GROWTH OF SHINY COWBIRD AND HOST CHICKS ..... *James W. Wiley* 126
- AUTUMN SANDHILL CRANE HABITAT USE IN SOUTHEAST OREGON ..... *Carroll D. Littlefield* 131
- DIETS OF HOUSE SPARROWS IN URBAN AND RURAL HABITATS *Ann P. Gavett and James S. Wakeley* 137
- VEGETATION STRUCTURE AND VESPER SPARROW TERRITORY LOCATION ..... *J. Michael Reed* 144
- MALE AND FEMALE PARENTAL CARE IN TREE SWALLOWS ..... *Terry E. Quinney* 147
- EXTRAPAIR COPULATIONS IN THE TREE SWALLOW ..... *Michael P. Lombardo* 150
- POLYGYNY IN THE YELLOW WARBLER ..... *Dominick A. DellaSala* 152
- TWO MALE BOBOLINKS FEED YOUNG AT THE SAME NEST ..... *Eric K. Bollinger, Thomas A. Gavin, Catherine J. Hibbard, and J. Timothy Wootton* 154
- CONSPECIFIC NEST TAKEOVERS AND EGG DESTRUCTION BY WHITE IBISES ..... *Peter Frederick* 156
- WINTER DIETS OF VULTURES IN SOUTHCENTRAL PENNSYLVANIA *Richard H. Yahner, Gerald L. Storm, and Anthony L. Wright* 157
- BREEDING BIOLOGY OF THE SEYCHELLES BLACK PARROT (*CORACOPSIS NIGRA BARKLYI*) *Robert E. Merritt, Patricia A. Bell, Victorin Laboudallon* 160
- ADDITIONS TO RECORDS OF NORTH AMERICAN AVIFAUNA IN YUCATÁN, MEXICO *David T. Rogers, Jr., Jesús Garcia B., and Antonio Rógel B.* 163
- CHOICE OF NEST BOXES BY CAVITY-NESTING DUCKS *Harry G. Lumsden, Judy Robinson, and Ronald Hartford* 167
- ROCK DOVES NESTING IN TREES ..... *A. Townsend Peterson* 168
- A NEW METHOD FOR COLLECTING PREY DELIVERED TO TUFTED PUFFIN CHICKS ... *Pat Baird* 169
- LAUGHING GULL NESTING ATTEMPT ON LAKE ERIE *Elliot J. Tramer and Louis W. Campbell* 170
- ADULT MALE BLUE GROUSE EATS LIZARDS ..... *Lee H. Simons* 171

ORNITHOLOGICAL LITERATURE ..... 173

ANNOUNCEMENT ..... 100

ERRATA ..... 92

# The Wilson Bulletin

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Razorbills *(Alca torda)*. The painting, in pastels and pencil with watercolor, is by Karen Allaben-Confer, winner of the 1985 George Miksch Sutton Award for Ornithological Art.

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# WAX DIGESTION IN WILSON'S STORM-PETREL

BRYAN S. OBST[1]

ABSTRACT.—Captive Wilson's Storm-Petrels (*Oceanites oceanicus*) fed a diet of pure wax (hexadecyl oleate) or triacylglycerol (olive oil) increased in body mass or lost mass more slowly than birds given only water, depending upon the quantity of lipid they were fed. Lipids extracted from the feces of wax-fed birds contained fatty alcohol and fatty acid, the products of wax hydrolysis. The data indicate the ability to digest waxes in this species. Waxes are abundant constituents of many marine organisms and form the majority of total lipid ingested by some seabird species. The ability to digest wax represents an important adaptation for marine birds that encounter waxy prey, allowing a vast source of potential energy to be utilized. *Received 9 July 1985, accepted 21 Oct. 1985.*

In terrestrial environments, animals typically store energy in the form of triacylglycerols (TAGs), and predators often derive much of their energy from the conversion of these lipids. In marine environments, however, many animals store energy in the form of wax esters (waxes), particularly in cold and deep water environments (Sargent et al. 1976). Waxes result from the esterification of a long-chain fatty alcohol with a single fatty acid. Many are liquid at room temperature, and all have an energy content similar to that of TAGs (40 kJ/g). It has been estimated that up to half of all the organic matter synthesized by the world's phytoplankton is converted at some time into wax (Benson and Lee 1975). There exists a huge standing crop of wax in the world's oceans. Wax storage is widespread at all levels of the food chain, and waxes are present in many marine organisms that are eaten by seabirds, including copepods, euphausiids, midwater cephalopods, and myctophid fishes (Sargent et al. 1976). Procellariiform birds accumulate dietary lipids in the proventriculus as stomach oil (Clarke and Prince 1976), and chemical analysis of these stomach

[1] Dept. Biology, Univ. California, Los Angeles, California 90024.

TABLE 1
THE RELATIVE IMPORTANCE OF TRIACYLGLYCEROL (TAG) AND WAX ESTERS (WAX) IN STOMACH OILS OF 24 PROCELLARIIFORM SPECIES[a]

| | TAG | Wax |
|---|---|---|
| Present in sample | 23 (96%)[b] | 20 (83%) |
| Most abundant constituent | 11 (46%) | 11 (46%) |
| Percent of total sample | 0–80% | 0–81% |

[a] Data are taken from a summary of the chemical compositions of stomach oils in Jacob (1982).
[b] Number of species (% of species).

oils provides a convenient index of the types of lipids ingested by the birds. In 24 procellariiform species whose stomach oil constituents have been identified and quantified (Jacob 1982), waxes were of roughly equal importance to TAGs (Table 1). In almost half of these species, wax was the most abundant class of lipids present in stomach oil. Thus, if they can be digested, waxes represent a potentially important energy source for marine birds.

Waxes tend to be inert compounds metabolically, even within the marine organisms that synthesize them (Lee and Barnes 1975). Vertebrate lipases hydrolyze waxes at a fraction of the rate they hydrolyze TAGs (Mattson et al. 1970, Savary 1971, Patton et al. 1975). In laboratory mice, diets containing greater than 1% wax by weight result in diarrhea, weight loss, or death (Verbiscar et al. 1980). Although waxes are the primary constituents of blubber and spermaceti in odontocete whales (Hansen and Cheah 1969), waxes have not been found in the tissues of marine birds (Clarke, in press). Thus, the fate of these energy-rich lipids ingested by birds is of interest. An inability to handle dietary wax quickly and efficiently would increase the rates of prey capture needed to satisfy energy requirements of foraging seabirds, and possibly render whole species of prey inedible.

Among terrestrial birds, the ability to digest wax has been previously demonstrated for the honeyguides (Indicatoridae; Friedmann and Kern 1956). Here, I present evidence that the Wilson's Storm-Petrel (*Oceanites oceanicus*) is able to digest wax and use the chemical potential energy stored within wax molecules.

## METHODS

Experiments were performed at Palmer Station, Anvers Island (64°46′S, 64°03′W), near the Antarctic Peninsula. Wilson's Storm-Petrels were captured at the nest and held in one-gallon containers fitted with a wire-mesh floor through which their droppings could fall. Birds were force-fed by packing a syringe with liquid or homogenized food (see below) and

forcing it under slight pressure through a tube inserted past the glottis and into the stomach. Beginning one day after capture, all birds were fed 5 ml of homogenized krill (*Euphausia superba*) every 8 h. This feeding regime was maintained for 48 h to make certain that the birds had adjusted to the procedure and were maintaining body mass on a forced diet.

Four birds were then switched to experimental diets. One bird was fed 1 ml wax (hexadecyl oleate) with 4 ml water; a second bird was fed 1 ml of TAG (olive oil) with 4 ml water; and the remaining two birds were given 5 ml water. All birds were fed every 8 h. Each individual was weighed to the nearest 0.1 g immediately prior to feeding. After 56 h, the diets were again adjusted. The volume of lipid administered to both the wax-fed and TAG-fed birds was doubled; their new diets were 2 ml hexadecyl oleate with 3 ml water, and 2 ml olive oil with 3 ml water, respectively. The two birds previously given only water were switched to a diet including wax (2 ml hexadecyl oleate with 3 ml water). Thus, all birds received 5 ml of liquid every 8 h throughout the experiment, and only the composition of the liquids varied.

Droppings from each bird were collected daily and frozen. Fecal lipids were later extracted with methanol and chloroform according to the methods of Bligh and Dyer (1959). Extracted lipids were dissolved in ethyl ether (anhydrous), and the lipid families present were separated via thin-layer chromatography on silica-gel coated plates in a developing solution of petroleum ether, ethyl ether, and acetic acid (80:20:1). The plates were dipped briefly in a cupric acetate solution and charred at 130°C to make lipid bands visible. Bands were identified by comparison with a set of purified, commercial standards (Nu Chek Prep No. 18-5 C, containing cholesterol, cholesterol oleate, triolein, oleic acid, and lecithin, with hexadecyl oleate added).

## RESULTS

*Changes in body mass.*—In the early part of the experiment, all four birds lost mass steadily (Fig. 1). However, the mean rate of mass loss in the birds receiving only water (3.85 g/day) was higher than that of either the wax-fed bird (2.19 g/day) or the TAG-fed bird (1.93 g/day). Rates of mass loss of the wax-fed and TAG-fed storm-petrels were very similar. When the volume of lipid administered was doubled, the decline in body mass was reversed; all four birds actually regained some of the body mass previously lost. The wax-fed storm-petrels showed a mean gain of 0.63 ± 0.28 g/day [SE] (N = 3) or 0.12 g body mass/g lipid fed, while the TAG-fed bird gained 2.29 g/day, or 0.42 g body mass/g lipid fed.

*Fecal lipids.*—In wax-fed birds, the total mass of lipid extracted from the feces averaged 3.2 ± 1.4% (N = 3) of the total lipid ingested. Mass of fecal lipids averaged 1.4 ± 0.5% (N = 2) of the lipid fed to TAG-fed birds. Analysis of fecal lipids (Fig. 2) from wax-fed birds revealed the presence of fatty alcohol and fatty acids, the end products of wax hydrolysis, as well as undigested wax. The prevalence of fatty alcohol in the feces was generally correlated with the quantity of wax fed to the bird during the 24-h period over which the feces were collected. Fecal lipids from TAG-fed birds included no fatty alcohols. However, the products of TAG hydrolysis, i.e., fatty acids and glycerol, were present, along with small quantities of TAG.

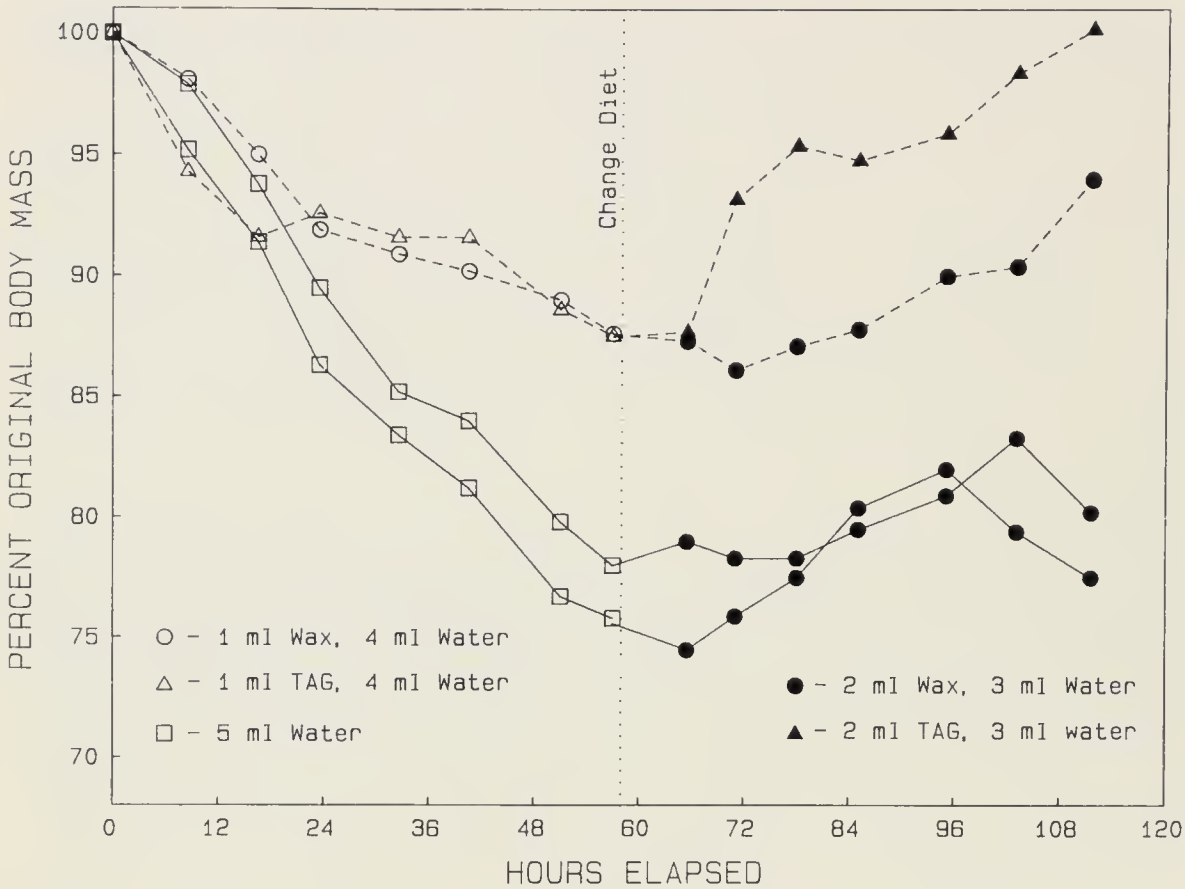


FIG. 1. Change in body mass of captive Wilson's Storm-Petrels fed diets of wax (hexadecyl oleate), TAG (olive oil), and water.

## DISCUSSION

The Wilson's Storm-Petrel is an opportunistic feeder, taking such wax-rich items as myctophid fishes and midwater squids from the cold waters of its breeding range (Obst, unpubl. data). The ability to maintain or add body mass on a pure wax diet, along with the presence of the products of wax hydrolysis in the feces, indicates that the Wilson's Storm-Petrel can digest wax. The presence of fatty alcohols in the feces does not in itself establish that this species is capable of using waxes as food, since microbial hydrolysis of wax esters in the hindgut could presumably liberate fatty alcohols without making them available to the host. However, the ability to maintain body weight on diets of either wax or TAG demonstrates that both of these lipids represented an energy souce for the captive storm-petrels in this experiment. The ability to digest waxes would be an important adaptation for any seabird that commonly encounters wax-rich prey. It would prevent a large source of chemical potential energy from going unused, and allow such prey to pass through the gut without producing a laxative effect.

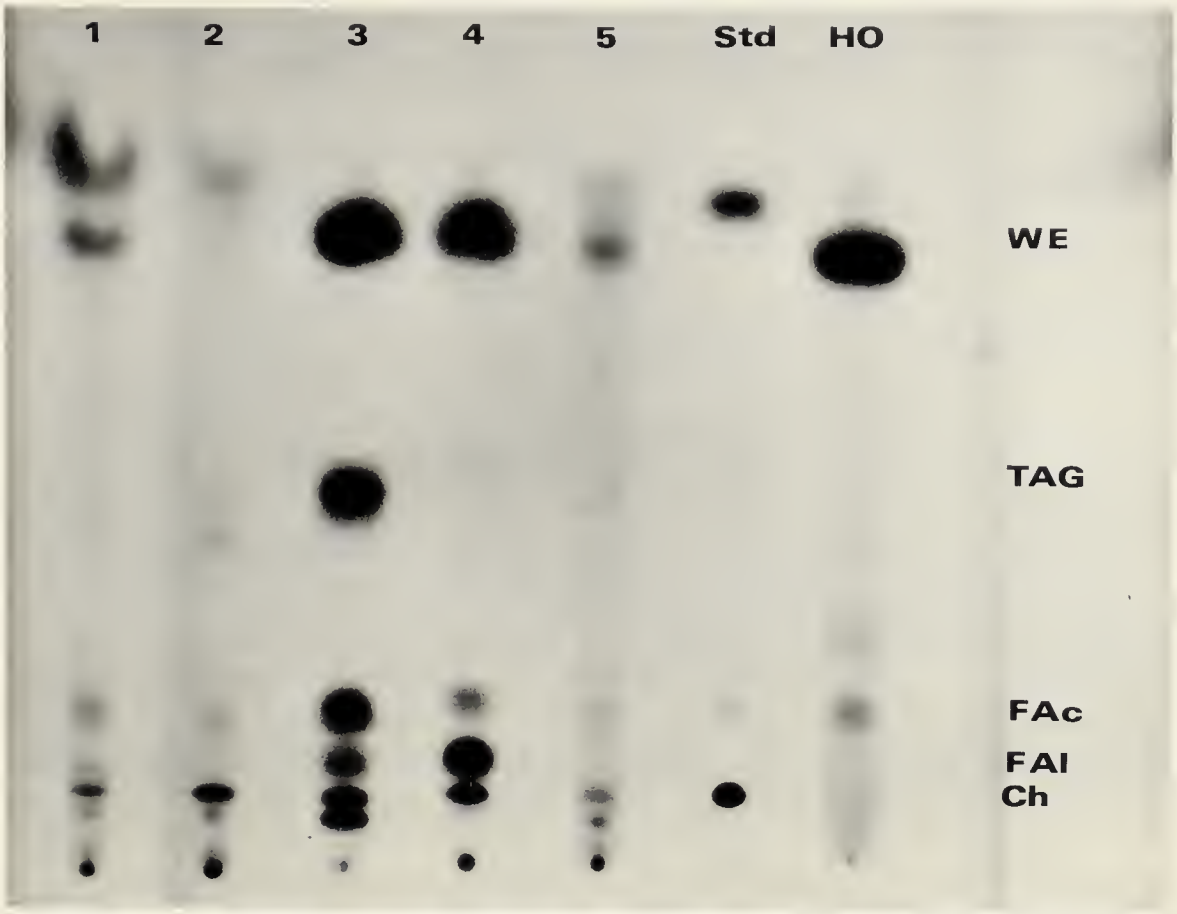


FIG. 2. Thin-layer chromatography of lipids extracted from feces of wax-fed and TAG-fed Wilson's Storm-Petrels. Lanes 1–5 represent individuals fed the following diets: Lane 1—3 ml wax/day; Lane 2—3 ml TAG/day; Lane 3—3 ml wax and 3 ml TAG/day; Lane 4—6 ml wax/day; Lane 5—3 ml wax/day, followed by a 24-h fast. Abbreviations are: WE = wax ester; TAG = triacylglycerol; FAc = fatty acid; FAl = fatty alcohol; Ch = cholesterol; HO = hexadecyl oleate (dietary wax); Std = standard, containing purified sterol ester, triacylglycerol, fatty acid, and cholesterol.

Rates of mass change appeared to be similar in wax-fed and TAG-fed storm-petrels when the birds were underfed, but TAG appeared to be used more efficiently than wax when provided in excess of the birds' energy requirements. Although the sample size upon which these observations are based is small, this interpretation is consistent with studies from other vertebrates that indicate that the hydrolysis of waxes proceeds at a slower rate than the hydrolysis of TAGs. Given a sufficiently long residence time in the gut, waxes might be digested completely, but rates of fat deposition would be relatively higher for birds on diets rich in TAGs if waxes are, indeed, digested more slowly. This could have important consequences for the growth rates of seabird chicks receiving wax-rich foods from their parents. However, conversion of wax to TAG requires

a suitable source of glycerol, and the substrates normally converted into glycerol, glucose, and amino acids were not present in these experimental diets.

Although the majority of procellariiform species represented in Table 1 inhabit high latitudes, there is good reason to expect that low-latitude seabirds also ingest much wax. Midwater fishes and cephalopods known to be rich in wax are common prey for many tropical seabirds, which capture them as these prey are driven to the surface by other predators (e.g., tuna, porpoises) or as they migrate to the surface at night (Ashmole 1971, Imber 1976). Sphenisciform, pelecaniform, and charadriiform species, as well as the procellariiforms, undoubtedly encounter waxy prey. The ability or inability to digest wax could be a factor shaping patterns of prey selection, feeding rates, and growth rates of marine birds inhabiting waters where wax-bearing prey occur. In feeding experiments using radiolabeled lipid tracers, D. Roby et al. (unpubl. data) found evidence for wax digestion in 4 high-latitude, planktivorous seabird species (3 petrels and an alcid). Further work should be undertaken to determine how widespread wax digestion is among seabirds, using species representing a variety of families and oceanographic regions.

## ACKNOWLEDGMENTS

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## COLOR PLATE

The Frontispiece painting "Razorbills" (*Alca torda*) has been made possible by an endowment established by George Miksch Sutton (1896–1982). The painting is by Karen Lynn Allaben-Confer, winner of the first George Miksch Sutton Award for Ornithological Art. (See announcement on page 333).

*Wilson Bull.*, 98(2), 1986, pp. 196–213

# FORAGING PATTERNS OF FOREST BIRDS: MALE-FEMALE DIFFERENCES

RICHARD T. HOLMES[1]

ABSTRACT.—Foraging patterns of males and females of nine arboreal passerine bird species that occur syntopically in a northern hardwoods forest in New Hampshire were compared intra- and interspecifically. Males and females of each species were similar in morphology but often differed in foraging heights, use of foraging maneuvers and substrates, tree species in which foraging occurred, and in positions within trees where they attacked prey. Overall, intraspecific intersexual differences were less than interspecific ones. Two exceptions were the Scarlet Tanager (*Piranga olivacea*) and Rose-breasted Grosbeak (*Pheucticus ludovicianus*), in which males of the two species were more similar to each other in methods of food exploitation than they were to conspecific females. This finding indicates the need to consider intraspecific (especially intersexual) variability, as well as interspecific differences, in studies of resource use and niche relations among forest birds.

Although differences between the sexes result in some resource partitioning within species, they are best explained by the hypothesis that birds forage locally near their centers of activity, which for passerine birds in the breeding season differ for males and females. Male foraging heights were positively correlated with song perch heights, as were female foraging heights with nest heights. Foraging heights of males, however, were not always higher than those of females, nor were mean song perch heights always higher than nest sites. Environmental factors such as local variations in the vertical distribution of plant species, vegetation structure, food availability, and predation are discussed as factors that affect the height at which these activities, and thus foraging, take place. *Received 24 Sept. 1985, accepted 22 Nov. 1985.*

Most attempts to characterize the foraging relations and associated niche characteristics of forest birds have not taken into account intraspecific variation in foraging, such as differences between the sexes (e.g., Rabenold 1978, Eckhardt 1979, Holmes et al. 1979, Landres and MacMahon 1983, Airola and Barrett 1985). This is due largely to the difficulties of clearly identifying in the field the sex of rapidly foraging individuals of the often monomorphic and monochromatic species occupying these habitats. Obtaining sufficient sample sizes for each sex can also be a problem.

Investigations of single species or small guilds, however, have shown that foraging patterns of males and females often differ, e.g., in species of woodpeckers (Kilham 1965, 1970; Selander 1966; Ligon 1968; Jackson 1970; Williams 1980), nuthatches (McEllin 1979, but see Grubb 1982), vireos (Williamson 1971), muscicapid flycatchers (Bell 1982), and several

[1] Dept. Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755.

parulid warblers (Morse 1968, 1971, 1980; Busby and Sealy 1979; Morrison 1982; Franzreb 1983). The explanations most often given for such differences are that they represent either (1) the results of intraspecific resource partitioning (Rand 1952, Selander 1966, Robbins 1971) or (2) the operation of foraging constraints associated with reproductive or other sex-related activities, such as localized feeding of males near song perches and of females near nest sites (Morse 1968, 1980; Williamson 1971; Franzreb 1983).

The purposes of this paper are (1) to examine the foraging patterns and ecology of males and females of the nine most common species of arboreally foraging birds that occur syntopically during the breeding season in a northern hardwoods forest in central New Hampshire, and (2) to contrast intraspecific, intersexual patterns with those occurring between species. Specifically, do males and females of the same species exploit food resources in ways more similar to each other compared to those exhibited by other co-occurring species? If intraspecific differences exist, do they represent resource partitioning, the results of foraging constraints, or both?

## STUDY AREA AND METHODS

The study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, on the 10-ha gridded census plot described by Holmes and Sturges (1975). The forest consists of second-growth northern hardwoods, with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula allegheniensis*) predominating. Occasional white ash (*Fraxinus americana*) and red spruce (*Picea rubens*) also occur. Canopy height averages about 25 m. The understory consists of saplings of the dominant tree species (except yellow birch), striped and mountain maples (*A. pensylvanicum* and *A. spicatum,* respectively), hobblebush (*Viburnum alnifolium*), a common fern (*Dryopteris spinulosa*), and various forbs.

Degrees of sexual dimorphism were assessed from measurements of weights, wing lengths, and culmen lengths of the males and females of each species. The first two of these measurements are often used as indicators of body size (Hamilton 1961), and the third is sometimes associated with differences in foraging between the sexes (Selander 1966). All weights were of live birds captured in mist nets on the study area during the breeding period and measured with Pesola scales (0.5-g accuracy). Weights of females caught prior to 16 June and of others known or suspected to be egg laying were excluded from the data set. Culmen and wing lengths of males and females of each species were measured with dial calipers (to 0.1 mm), either on live birds at Hubbard Brook or on specimens in the American Museum of Natural History that had been collected in summer in New England.

Foraging patterns of males and females were quantified between mid-June and mid-July in summers from 1974 to 1978. This coincided with the nestling and early fledging stage of the breeding cycle, which was the time when birds were foraging most actively and when food may have been scarcest (Holmes et al. 1979; R. T. Holmes, unpubl. data). The sex of each bird under observation was determined either by plumage (warblers, tanager, grosbeak) (see Table 1 for species considered in this study) or by the presence of unique individually coded color bands (all species, but especially the flycatcher and vireos). Color bands were

TABLE 1

MENSURAL CHARACTERISTICS OF MALE AND FEMALE PASSERINES AT HUBBARD BROOK

| Bird species | Sex | Characteristic | | |
|---|---|---|---|---|
| | | Field weight (g)[a] | Culmen length (mm) | Wing length (mm) |
| Least Flycatcher (*Empidonax minimus*) | M | 10.2 ± 0.7 (54)[b] | 7.5 ± 0.2 (7)[a] | 62.1 ± 0.5 (5)[a] |
| | F | 9.9 ± 1.3 (95)[c] | 7.3 ± 0.4 (14)[a] | 60.0 ± 2.9 (13)[a,c] |
| Red-eyed Vireo (*Vireo olivaceus*) | M | 17.2 ± 1.0 (112) | 9.6 ± 0.3 (21)[a] | 80.0 ± 2.2 (18)[a] |
| | F | 17.2 ± 1.3 (111) | 9.4 ± 0.5 (25)[a] | 78.0 ± 1.8 (23)[a,d] |
| Philadelphia Vireo (*V. philadelphicus*) | M | 11.4 ± 0.7 (13) | 7.2 ± 0.2 (5) | 66.2 ± 2.4 (5) |
| | F | 12.0 ± 1.6 (13) | 6.8 ± 0.2 (5)[d] | 66.5 ± 1.2 (5) |
| Black-throated Blue Warbler (*Dendroica caerulescens*) | M | 9.8 ± 0.5 (70) | 7.3 ± 0.2 (11)[a] | 63.8 ± 2.5 (9)[a] |
| | F | 10.1 ± 0.9 (55)[c] | 7.2 ± 0.3 (7)[a] | 60.4 ± 0.5 (6)[a,d] |
| Black-throated Green Warbler (*D. virens*) | M | 9.2 ± 0.5 (26) | 7.3 ± 0.3 (6) | 61.5 ± 0.9 (6) |
| | F | 9.3 ± 0.6 (28) | 7.1 ± 0.2 (5) | 59.0 ± 1.5 (4) |
| Blackburnian Warbler (*D. fusca*) | M | 9.8 ± 0.6 (15) | 7.2 ± 0.2 (5) | 67.9 ± 2.0 (5) |
| | F | 10.4 ± 0.9 (12) | 7.3 ± 0.3 (5) | 64.6 ± 2.9 (5) |
| American Redstart (*Setophaga ruticilla*) | M | 8.6 ± 0.5 (71) | 6.9 ± 0.3 (13)[a] | 63.2 ± 1.7 (10)[a] |
| | F | 8.7 ± 0.6 (80) | 6.9 ± 0.3 (12)[a] | 59.5 ± 2.0 (9)[a,e] |
| Scarlet Tanager (*Piranga olivacea*) | M | 28.7 ± 1.8 (22) | 10.4 ± 0.6 (5) | 94.5 ± 2.5 (5) |
| | F | 29.6 ± 1.8 (30) | 9.9 ± 0.5 (5) | 91.3 ± 2.7 (5) |
| Rose-breasted Grosbeak (*Pheucticus ludovicianus*) | M | 43.6 ± 2.8 (18) | 10.1 ± 0.9 (5) | 104.5 ± 3.4 (5) |
| | F | 45.5 ± 2.9 (21) | 10.4 ± 0.5 (6) | 99.1 ± 4.1 (6)[c] |

[a] Measurements from live adult birds captured in mist nets at Hubbard Brook.
[b] $\bar{x} \pm$ SD (N).
[c] Female differs from male ($t$-test, $P < 0.05$).
[d] Female differs from male ($t$-test, $P < 0.01$).
[e] Female differs from male ($t$-test, $P < 0.001$).

placed on birds caught in mist nets that were operated weekly each season as part of censusing procedures (see Holmes and Sturges 1975). By the end of each nesting season, more than 80% of the adult birds on the study area were individually marked. Mist-netted birds were sexed by the presence of a cloacal protuberance (male) or brood patch (female), following the procedures of Wood (1969) and the U.S. Fish and Wildlife Service Banding Manual (1977).

Methods used to quantify bird foraging behavior have been described by Holmes et al. (1979). Briefly, individual birds were followed for as long as they could be kept in sight (usually <2 min), and all attempts to capture prey were recorded. For each prey-attack, we

noted the maneuver used (glean, hover, hawk; see below), the substrate to which it was directed (bark, leaf, ground, air), the plant species when appropriate, the height above ground, and, if in a tree, whether it was proximal to the main axis (trunk) or distal (along the outer halves of branches). At least six to eight individuals of each sex per species, and often more for the more common species, were observed each season.

Data on nest heights were collected in the summers of 1969 through 1979 in the study area. Heights of song perches used by males were estimated in June 1983 and 1984. For these, the height of a singing male was recorded once per encounter, except for the less-common species, for which up to five records were taken per individual at intervals of not less than 5 min.

Two statistical tests were used to compare males and females within species. Differences between means (weights, morphological measurements, foraging heights) were analyzed with Student's *t*-tests. Differences between frequency distributions (foraging maneuvers, tree species use, foraging height distributions, foraging locations within trees) were compared with *G*-tests (Sokal and Rohlf 1981). The level of significance was 0.05 (see Discussion). Overlap values of foraging height distributions were calculated using the method of Holmes and Pitelka (1968).

To compare foraging among sexes and species simultaneously, multivariate techniques were used on a matrix of 18 "species" (rows) by 22 "characters" (columns), following the procedures of Holmes et al. (1979). In this case, the "species" represent males and females of nine passerine bird species. The characters are similar to the categories used in the earlier analysis (Holmes et al. 1979), except that maneuvers directed towards the ground, tree trunks, and other actions infrequently used by these foliage-foragers were omitted. In the present analysis, the 22 characters included nine maneuver-substrate categories, proportional use of eight plant species, two foraging location categories (proximal vs distal), mean foraging height, standard deviation of foraging height, and mean body weight. The justifications for selecting these characters are given in Holmes et al. (1979). The first 19 characters represent use frequencies of foraging categories and were log-transformed to reduce skewness. All 22 columns were standardized to bring means to 0 and variances to 1.0 (see Holmes et al. 1979), the effect of which is to weight all categories equally. The 22 × 18 "species" matrix (Q-technique of Sneath and Sokal 1973) was used to calculate the Euclidean distances between all combinations of the 18 "species" in the multidimensional space defined by the 22 characters. This distance matrix was then subjected to hierarchical cluster analysis (maximum method, Johnson 1967) to illustrate graphically the similarities and differences in foraging among the sexes and species of these forest birds.

## RESULTS

### The Species and Their Intersexual Morphological Differences

The nine species of passerine birds at Hubbard Brook considered in this paper consisted of a tyrannid flycatcher, two vireos, four parulid warblers, a tanager, and a grosbeak (Table 1). All take more than 50% of their prey from tree foliage and comprise the major component of the foliage-gleaning-hovering guild in this forest (Holmes et al. 1979). Three species (Least Flycatcher, Red-eyed Vireo, Philadelphia Vireo) are sexually monochromatic, and the other six are sexually dichromatic, with males having brighter coloration than females. All have basically monogamous breeding systems (Ford 1983).

Measurements of body weights, culmen lengths, and wing lengths of the males and females of these nine species were examined for evidence of sexual dimorphism (Table 1). Only the Least Flycatcher and Black-throated Blue Warbler exhibited statistically significant differences in weight between the sexes (Table 1), with the male being heavier in the flycatcher, and the female heavier in the warbler. In both cases, these differences amounted to <3%. Intersexual differences in wing lengths were more frequent, with the males of six species having significantly longer wings than their respective females. Differences, however, were small (6% or less), relative to those occurring among "strongly dimorphic" species such as raptors or some icterids (Selander 1966). The only species to show a significant sex-related difference in culmen length was the Philadelphia Vireo. In that species, males had a slightly longer bill (Table 1).

Thus, for these species overall, only minor sexual dimorphism is evident, and the differences that exist do not seem to be sufficient to have major effects on food capturing abilities or other aspects of food resource exploitation.

## Use of Vertical Strata

*Foraging heights.*—Mean foraging heights of males and females of all but one species ranged between 10 and 15 m (Table 2). The large standard deviations of foraging heights (Table 1) and broad foraging-height profiles (Fig. 1) of each sex of these eight species indicate that they foraged over practically the entire vertical profile of this forest. The single species with a relatively narrow foraging height range was the Black-throated Blue Warbler. It foraged primarily in the shrub and sapling layers; males at an average height of 6 m and females at 3 m (Table 2) (Fig. 1).

For three species (Least Flycatcher, American Redstart, Blackburnian Warbler), mean foraging heights of males and females were statistically similar, while in six, significant intersexual differences were found (Table 2). In four of these (Red-eyed Vireo, Black-throated Green Warbler, Scarlet Tanager, Rose-breasted Grosbeak), females foraged higher than males, and in two (Philadelphia Vireo and especially the Black-throated Blue Warbler), males foraged higher than females (Table 2).

Because the vertical foraging distributions of these birds often were not distributed normally (Fig. 1), comparisons of means are not always valid. Therefore, I compared the intersexual distributions of foraging heights (see Fig. 1) using $G$-tests (Sokal and Rohlf 1981). The results showed significant differences ($P < 0.01$) in the use of strata for foraging by males and females of all species except the grosbeak (Table 2). Three species showed significant differences in foraging height distributions but had statistically similar mean foraging heights. In the redstart and especially

TABLE 2

VERTICAL DISTRIBUTION (M) OF FORAGING, SINGING, AND NESTING BY MALE AND FEMALE PASSERINES AT HUBBARD BROOK

| Bird Species | Sex | Foraging heights | % Overlap[a] | Song perch heights | Nest heights |
|---|---|---|---|---|---|
| Least Flycatcher | M | 10.5 ± 4.2 (287)[b] | 79.2[f] | 7.5 ± 2.3 (20) | 11.8 ± 4.8 (85) |
| | F | 10.4 ± 4.8 (324) | | | |
| Red-eyed Vireo | M | 11.8 ± 4.5 (739) | 87.9[f] | 14.5 ± 4.6 (57) | 10.7 ± 5.8 (31) |
| | F | 12.5 ± 4.3 (424)[d] | | | |
| Philadelphia Vireo | M | 14.6 ± 6.2 (388) | 78.9[f] | 15.9 ± 4.9 (45) | 24.0 ± 4.6 (14) |
| | F | 13.5 ± 7.3 (195)[c] | | | |
| Black-throated Blue Warbler | M | 5.9 ± 3.8 (884) | 62.7[f] | 8.1 ± 3.8 (47) | 0.5 ± 0.2 (17) |
| | F | 3.3 ± 3.0 (470)[e] | | | |
| Black-throated Green Warbler | M | 13.1 ± 5.2 (442) | 78.7[f] | 15.1 ± 2.6 (36) | 11.3 ± 4.0 (9) |
| | F | 15.2 ± 4.0 (270)[e] | | | |
| Blackburnian Warbler | M | 15.1 ± 3.5 (324) | 72.8[f] | 13.4 ± 4.1 (23) | 7.3 ± 3.2 (3) |
| | F | 14.4 ± 4.8 (320) | | | |
| American Redstart | M | 10.9 ± 4.8 (1111) | 88.6[f] | 11.1 ± 2.9 (33) | 7.4 ± 4.4 (70) |
| | F | 11.3 ± 4.6 (510) | | | |
| Scarlet Tanager | M | 11.7 ± 4.8 (303) | 59.8[f] | 15.5 ± 4.9 (33) | 12.8 ± 3.2 (8) |
| | F | 14.8 ± 4.5 (137)[e] | | | |
| Rose-breasted Grosbeak | M | 10.8 ± 5.3 (189) | 81.4 | 12.0 ± 4.8 (26) | 14.5 ± 8.8 (12) |
| | F | 12.9 ± 5.4 (99)[d] | | | |

[a] Overlap between male and female foraging distributions (see Fig. 1), calculated by 2-m intervals using the method of Holmes and Pitelka (1968).
[b] $\bar{x}$ ± SD (N).
[c] Female differs from male ($t$-test, $P < 0.05$).
[d] Female differs from male ($t$-test, $P < 0.01$).
[e] Female differs from male ($t$-test, $P < 0.001$).
[f] Female differs from male ($G$-test, $P < 0.01$).

the Blackburnian Warbler, females used a higher stratum proportionately more often than did males (Fig. 1), resulting in significantly different profiles, even though mean heights were not statistically different (Table 2). The opposite pattern was found for the Least Flycatcher: females used a lower stratum more frequently than males (Fig. 1). In every case, however, the overlap in vertical foraging distribution between males and females of each species was extensive (Fig. 1), ranging from 62% in the Black-throated Blue Warbler to 89% in the American Redstart (Table 2).

*Song perch and nest heights.*—Heights at which males sang ranged from an average of 8.1 m for the Black-throated Blue Warbler to 15.9 m for the Philadelphia Vireo (Table 2). Mean heights of song perches correlated significantly with the mean foraging heights of males ($r = 0.74$, $P < 0.05$).

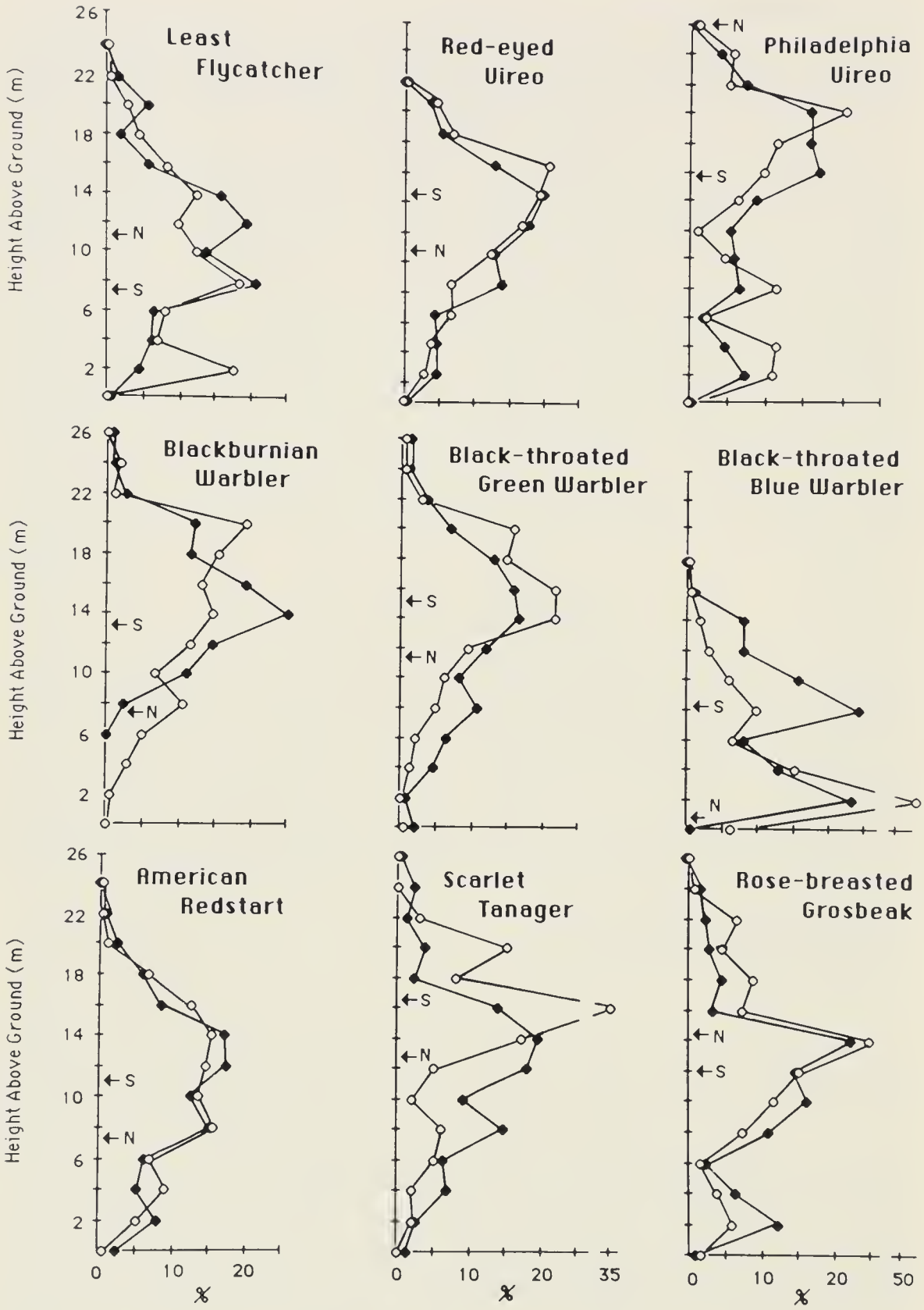


FIG. 1. Foraging height distributions by 2-m intervals for males (solid symbols) and females (open symbols) of nine passerines breeding in the Hubbard Brook forest. Sample sizes are given in Table 2. N = mean nest height and S = mean singing height of males (see Table 2).

They were slightly more correlated with the mean foraging heights of conspecific females ($r = 0.79$, $P < 0.05$).

Nesting heights varied from an average of 0.5 m for the Black-throated Blue Warbler to 24 m for the Philadelphia Vireo (Table 2). There was a positive but nonsignificant correlation between nest heights and foraging heights of females ($r = 0.62$, $P > 0.08$) and of males ($r = 0.62$, $P > 0.08$).

## Use of Foraging Substrates and Maneuvers

The foraging behavior of males and females of each species, as indicated by their prey-attack behavior and the substrates to which they were directed, was broadly similar (Table 3). Thus, both sexes of the two vireos, the flycatcher, redstart, Black-throated Blue Warbler, and tanager were primarily leaf hoverers, while male and female Black-throated Green Warblers, Blackburnian Warblers, and Rose-breasted Grosbeaks were mainly leaf gleaners. The second most common maneuver-substrate combination used was the same for both sexes in each species, except for the tanager, in which males gleaned and females hawked flying insects (Table 3). The second most common foraging action within each species was usually another leaf-directed attack (e.g., leaf gleaners hovered secondarily at leaves and vice versa), but for the flycatcher, redstart, and female tanager, it was hawking of flying insects. Despite overall similarities within species, there were significant intersexual differences in seven of the species in their use of maneuver-substrate categories. Only males and females of the Least Flycatcher and of the Philadelphia Vireo were statistically indistinguishable (Table 3).

## Foraging on Plant Species and Locations within Trees

Holmes and Robinson (1981) showed that many of the bird species at Hubbard Brook forage selectively among the different tree species in the forest, and similar observations have been reported for other forest birds (e.g., Franzreb 1983, Airola and Barrett 1985). When the foraging attack frequencies of males and females of Hubbard Brook birds are analyzed by major tree species to which they were directed (using only plant-directed prey-attacks), significant intersexual differences were found in all species except the Least Flycatcher and Scarlet Tanager (Table 4). Although the proportion of foraging maneuvers occurring in different tree species was basically consistent between males and females of each bird species, some differences occurred. Male Black-throated Green Warblers foraged on sugar maple and yellow birch about equally, while females used yellow birch more often than sugar maple (Table 4). Male grosbeaks foraged with about equal frequency on beech, sugar maple, and yellow birch, but females foraged more often on yellow birch, and seemed to

TABLE 3

USE OF FORAGING SUBSTRATES AND MANEUVERS BY MALE AND FEMALE PASSERINES AT HUBBARD BROOK

| | | | % Frequency | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Leaf | | Twig | | Branch | | Trunk | | Air | Ground |
| Bird species | Sex | N | Hover | Glean | Hover | Glean | Hover | Glean | Hover | Glean | Hawk | All[a] |
| Least Flycatcher | M | 262 | 72.5 | 1.9 | 0 | 0.4 | 0.4 | 0.4 | 0.4 | 0.4 | 23.2 | 0 |
| | F | 287 | 81.6 | 2.4 | 0 | 0.3 | 1.4 | 0 | 0 | 0 | 14.3 | 0 |
| Red-eyed Vireo | M | 664 | 50.2 | 33.4 | 2.4 | 1.8 | 1.1 | 2.9 | 2.0 | 0.9 | 5.3 | 0 |
| | F[b] | 397 | 44.8 | 42.5 | 0.5 | 0.5 | 1.3 | 1.3 | 0.5 | 0.3 | 8.3 | 0 |
| Philadelphia Vireo | M | 334 | 58.4 | 27.6 | 0 | 2.0 | 1.5 | 2.3 | 1.5 | 0.9 | 5.2 | 0.6 |
| | F | 169 | 55.0 | 30.2 | 0 | 1.2 | 1.8 | 4.1 | 0 | 0 | 7.7 | 0 |
| Black-throated Blue Warbler | M | 888 | 50.3 | 21.0 | 1.4 | 4.4 | 1.4 | 5.4 | 4.3 | 4.3 | 7.4 | 0.1 |
| | F[b] | 471 | 55.5 | 24.0 | 0.2 | 1.9 | 0.4 | 1.9 | 3.4 | 4.8 | 6.8 | 1.1 |
| Black-throated Green Warbler | M | 384 | 33.8 | 43.0 | 1.0 | 2.6 | 0.5 | 0.8 | 2.1 | 3.9 | 10.7 | 1.6 |
| | F[b] | 233 | 21.0 | 52.5 | 2.6 | 6.4 | 1.3 | 2.1 | 2.1 | 1.3 | 10.7 | 0 |
| Blackburnian Warbler | M | 283 | 18.8 | 56.5 | 0.4 | 3.5 | 0.4 | 3.1 | 1.4 | 7.8 | 8.1 | 0 |
| | F[c] | 254 | 27.0 | 49.1 | 0 | 8.8 | 0.4 | 1.3 | 1.8 | 1.3 | 10.3 | 0 |
| American Redstart | M | 911 | 47.4 | 16.1 | 0.1 | 0.2 | 0.2 | 3.3 | 0.7 | 0.9 | 30.7 | 0.4 |
| | F[b] | 432 | 60.4 | 15.0 | 0.2 | 0.5 | 0.5 | 0.5 | 0.2 | 0.2 | 22.5 | 0 |
| Scarlet Tanager | M | 166 | 34.9 | 28.9 | 0 | 1.2 | 3.1 | 8.4 | 6.0 | 2.4 | 14.5 | 0.6 |
| | F[c] | 81 | 34.6 | 28.4 | 0 | 0 | 0 | 4.9 | 1.2 | 0 | 30.9 | 0 |
| Rose-breasted Grosbeak | M | 280 | 26.4 | 47.5 | 0.4 | 2.1 | 1.1 | 3.2 | 6.4 | 6.4 | 6.1 | 0.4 |
| | F[c] | 128 | 34.2 | 51.6 | 0 | 1.6 | 0 | 1.6 | 1.6 | 1.6 | 6.3 | 2.3 |

[a] Includes all ground-directed maneuvers, such as gleans, hovers, probes, etc. Data in this column were not included in the multivariate analyses.
[b] Female differs from male ($G$-test, $P < 0.001$).
[c] Female differs from male ($G$-test, $P < 0.01$).

TABLE 4

FREQUENCY (%) OF FORAGING MANEUVERS DIRECTED TOWARDS PREY ON DIFFERENT PLANT SPECIES BY MALE AND FEMALE PASSERINES AT HUBBARD BROOK

| Bird species | Sex | N | Plant species | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Beech | Sugar maple | Yellow birch | White ash | Conifer | Other maple[a] | Viburnum | Herb-fern |
| Least Flycatcher | M | 235 | 23.1 | 35.7 | 35.7 | 0.4 | 0.9 | 3.8 | 0 | 0.4 |
| | F | 286 | 22.7 | 41.6 | 30.5 | 0.4 | 0.7 | 3.1 | 0 | 1.0 |
| Red-eyed Vireo | M | 697 | 29.4 | 44.9 | 20.9 | 2.0 | 1.3 | 1.5 | 0 | 0 |
| | F[b] | 390 | 29.5 | 35.6 | 26.9 | 5.4 | 0.5 | 2.1 | 0 | 0 |
| Philadelphia Vireo | M | 358 | 10.1 | 33.0 | 40.8 | 12.0 | 1.1 | 2.0 | 0 | 1.1 |
| | F[b] | 186 | 9.1 | 23.7 | 40.9 | 20.4 | 0.5 | 4.3 | 1.1 | 0 |
| Black-throated Blue Warbler | M | 873 | 33.0 | 32.4 | 10.3 | 0 | 2.5 | 12.9 | 8.7 | 0.2 |
| | F[b] | 470 | 30.2 | 25.4 | 9.4 | 0.4 | 2.3 | 10.2 | 18.7 | 3.4 |
| Black-throated Green Warbler | M | 389 | 10.0 | 38.6 | 39.8 | 0.8 | 9.3 | 1.5 | 0 | 0 |
| | F[c] | 242 | 4.5 | 12.4 | 74.4 | 0.4 | 5.0 | 2.9 | 0.4 | 0 |
| Blackburnian Warbler | M | 300 | 14.0 | 7.3 | 65.4 | 2.0 | 10.0 | 1.3 | 0 | 0 |
| | F[c] | 294 | 8.5 | 5.8 | 52.4 | 3.7 | 29.6 | 0 | 0 | 0 |
| American Redstart | M | 865 | 20.9 | 36.0 | 33.0 | 0.7 | 0.7 | 5.8 | 0.1 | 2.5 |
| | F[c] | 450 | 25.1 | 44.0 | 26.2 | 0.2 | 0.7 | 3.1 | 0 | 0.7 |
| Scarlet Tanager | M | 159 | 30.8 | 18.9 | 47.8 | 0.6 | 0 | 1.9 | 0 | 0 |
| | F | 73 | 28.8 | 12.3 | 45.2 | 2.8 | 8.2 | 2.7 | 0 | 0 |
| Rose-breasted Grosbeak | M | 282 | 31.6 | 29.1 | 31.0 | 0.7 | 0 | 5.3 | 1.4 | 0 |
| | F[c] | 125 | 8.0 | 29.6 | 47.2 | 12.0 | 1.6 | 1.6 | 0 | 0 |

[a] *Acer spicatum* and *A. pensylvanicum* (see Study Area and Methods).
[b] Female differs from male ($G$-test, $P < 0.01$).
[c] Female differs from male ($G$-test, $P < 0.001$).

TABLE 5

FREQUENCY OF PREY-ATTACKS BY MALE AND FEMALE PASSERINES[a] DIRECTED TOWARDS SUBSTRATES ALONG THE DISTAL HALVES OF BRANCHES OF CANOPY TREES

| Bird species | % Distal | |
|---|---|---|
| | Males | Females |
| Least Flycatcher | 78.9 (147)[b] | 79.9 (199) |
| Red-eyed Vireo | 58.5 (388) | 61.3 (253) |
| Philadelphia Vireo | 61.8 (152) | 70.3 (74) |
| Black-throated Green Warbler | 61.1 (167) | 74.2 (177)[c] |
| Blackburnian Warbler | 77.3 (185) | 80.0 (170) |
| American Redstart | 68.7 (419) | 64.7 (249) |
| Scarlet Tanager | 29.3 (99) | 64.6 (48)[c] |
| Rose-breasted Grosbeak | 51.0 (143) | 52.5 (61) |

[a] The Black-throated Blue Warbler is not included because it forages primarily among shrubs and saplings in the understory where the distinction between proximal and distal is not easily made.
[b] % (N).
[c] Females differ from males ($G$-test, $P < 0.01$).

avoid beech (Table 4). Female Black-throated Blue Warblers foraged more frequently than males on hobblebush, herbs, and ferns (Table 4). Finally, although male and female Blackburnian Warblers attacked prey predominately on yellow birch foliage, females attacked prey in conifers nearly a third of the time, considerably more than did males (Table 4). The latter is an example of high selectivity, because conifers in this forest are relatively rare (relative importance value = 1%, Holmes and Robinson 1981).

Males and females of each species foraged with equal frequency in the proximal and distal portions of canopy trees, except for the Black-throated Green Warbler and Scarlet Tanager (Table 5). (Black-throated Blue Warblers were not considered in this analysis; see footnote in Table 5.) In these two species, females foraged more often in the distal, and males more often in the proximal, parts of trees. This was especially pronounced in the tanager, in which males foraged 70% of the time in the inner portions of the trees (Table 5) and took insects relatively more often from bark than did females (Table 3). Female tanagers and all other species foraged most often in the distal portions of trees where most foliage (and thus foliage-dwelling insects) occurred.

## Inter- and Intra-specific Comparisons

The clustering of the males and females in multivariate space, based on 22 foraging-related characteristics (see Methods section), illustrates their similarities and differences in foraging both between sexes within species and between species within sex (Fig. 2). Despite many statistically

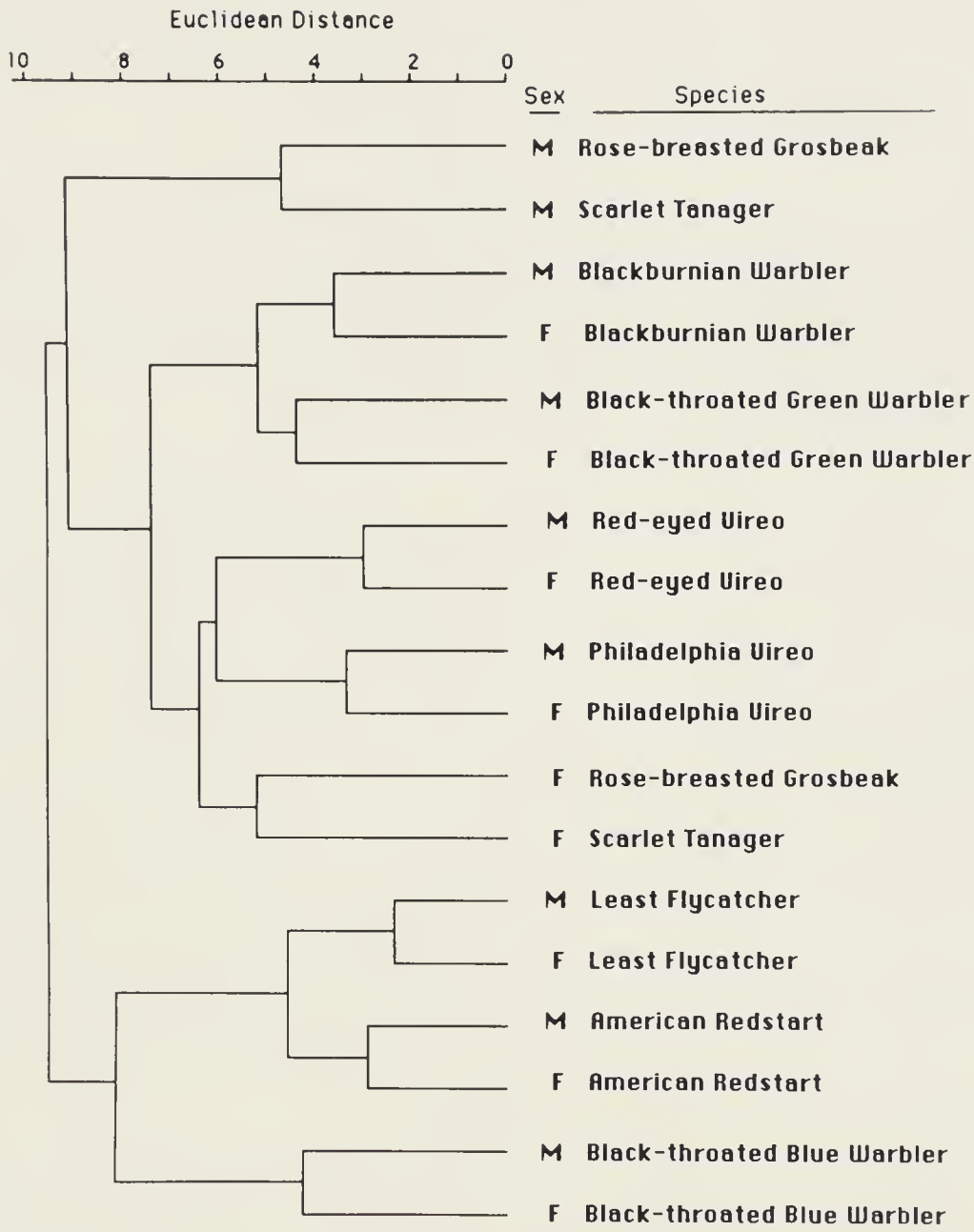


FIG. 2. Cluster dendrogram showing intersexual and interspecific relationships of nine passerine birds at Hubbard Brook, based on multivariate analyses of their foraging behavior.

significant intersexual differences in individual characteristics within species, conspecific males and females were generally more similar to each other than they were to other species. The two exceptions were the Scarlet Tanager and Rose-breasted Grosbeak, in which males were more similar to each other than to their respective females. The females of these two species were more closely aligned with the vireos than they were with the males of their own species (Fig. 2). These associations are due to the females of both species foraging, on average, higher in the canopy (Table

2) and more frequently in white ash (Table 4) than did males, while males of the two species attacked prey on trunks and branches more often than did females (Table 3).

## DISCUSSION

The results of this study indicate that considerable intersexual variation in resource exploitation exists within insectivorous bird species at Hubbard Brook, and that it occurs in the absence of any major morphological differences between the sexes. Before discussing the implications of these findings, two caveats concerning the statistical procedures and results need to be mentioned.

First, because many single statistical tests were performed, some may show significance simply by chance (i.e., a Type I error, Sokal and Rohlf 1981). However, even if a more stringent significance level were to be accepted (e.g., $P < 0.01$), most of the conclusions would hold (see Results). Secondly, and potentially more important, is the problem of "sacrificial pseudoreplication" that is coupled with the use of Chi-square (or $G$) tests (see Hurlbert 1984). When data are pooled prior to statistical analysis, as they were for the foraging parameters in this study, no measure of variance is possible and statistical results may be spurious. In the present study, the data came from a variety of individuals of both sexes observed during a three to four week period in each of several seasons. These features, along with the relatively large sample sizes, should swamp out the above sampling effects. Nevertheless, the statistical results for some of the differences between the sexes should be viewed with caution, and future studies should be designed to include proper replication and measures of variability. As far as I am aware, no published studies of bird foraging behavior have been so designed.

Two major hypotheses have been proposed to account for the existence of differences in foraging between male and female forest passerines. The first is that they have evolved as a result of, or to alleviate, intraspecific competition (Rand 1952, Selander 1966). Although the causal factors implicit in this hypothesis can not be tested adequately with available data (see above), the males and females of these species do often forage in different places or different ways, i.e., partition resources. Only the Least Flycatcher showed few intersexual differences (Tables 2–5). Sexes of other species differed in the use of at least two or more foraging categories, e.g., in foraging maneuvers, the heights at which they foraged, the plant species they searched for insects, and their positions of foraging within trees. Moreover, for species in which males and females foraged at the same heights (e.g., American Redstart), there were often differences in maneuver-substrate and tree species use, while among species in which

sexes foraged at different heights (e.g., Philadelphia Vireo), there were no differences in maneuver-substrate use.

Even though males and females often differed in patterns of food exploitation, they were generally more similar in their foraging behavior to each other than to other species. Similar findings were reported by Morse (1971) for *Dendroica* warblers in Maine. However, at Hubbard Brook, there were two exceptions to these patterns: male Scarlet Tanagers and Rose-breasted Grosbeaks were more similar to each other in how they foraged than they were to their conspecific females. Thus, studies of foraging behavior and niche relations should consider differences between the sexes in order to document accurately the ecological similarities and differences within forest bird guilds. This holds even if only a few species show such marked differences.

The second hypothesis for the existence of intersexual differences is that birds forage near their centers of activity, which for passerine birds in the breeding season differ between the sexes. The most frequent intersexual foraging difference reported in previous studies has been that males typically foraged higher than females (Morse 1968, Williamson 1971, Busby and Sealy 1979, McEllin 1979, Morrison 1982, Franzreb 1983, but see Grubb 1982 and Bell 1982). Some researchers have suggested that this is because males are more conspicuous and effective in long distance communication when they are at greater heights and that they feed near their song perches; likewise, females forage in lower strata near their nest sites (Morse 1968, 1980; Franzreb 1983; and others). The results from Hubbard Brook appear at first to contradict this hypothesis. Males of only two species foraged significantly higher than females, there were no significant differences in mean foraging heights between sexes in three species, and females foraged significantly higher than males in four species. The pattern was variable even for the *Dendroica* warblers, for which previous studies had indicated that males always foraged higher than females (Morse 1968, Busby and Sealy 1979, Morrison 1982, Franzreb 1983): at Hubbard Brook, males foraged significantly higher than females in only one species (Black-throated Blue); the pattern was reversed in another (Black-throated Green); and there was no significant difference in male-female foraging heights in the third (Blackburnian) (Table 2).

Nonetheless, male foraging heights for all nine species at Hubbard Brook were positively correlated with male song perch heights, and those of females with nest heights. Although nest height in six species averaged lower than the male's singing height, the differences were large only for the Black-throated Blue and Blackburnian warblers (Table 2). For the remaining three species and particularly the Philadelphia Vireo, nests were placed, on average, higher than male song heights (Table 2) (Fig. 1).

Most previous studies showing that males foraged higher than females (e.g., Morse 1968, McEllin 1979, Morrison 1982, Franzreb 1983, but not Williamson 1971) were conducted in coniferous or mixed deciduous-coniferous habitats. Males in these studies often sang from near the tops of conically-shaped, densely foliated conifers, and females nested lower in the thicker foliage (Morse 1980). In broad-leaved forests, such as those at Hubbard Brook, there is typically a dense, closed canopy, a relatively open subcanopy, an an understory that may vary in foliage density (see foliage density profile for the Hubbard Brook forest in Sherry 1979). In such habitats, as evidenced by the present study, birds often nest in dense foliage on or near the ground or in the canopy (Table 2), and males of many species forage and sing in the lower portions of the canopy and in the subcanopy (e.g., Least Flycatchers, American Redstarts, Black-throated Blue Warblers at Hubbard Brook, in particular) (Table 2). Thus, the principle that males forage in strata where they are relatively conspicuous and females forage near their nests applies to Hubbard Brook, but the particular structure of the forest influences the heights at which these events take place.

The fact that male and female passerines often forage at different heights (males higher than females or vice versa) means that each may encounter different foraging opportunities, which, in turn, may affect their foraging patterns (Robinson and Holmes 1982, 1984). Variability in foraging behavior among individual male and female American Redstarts has been attributed to local differences in vegetation structure and food availability on different territories (Holmes et al. 1978). Similar differences may occur within territories in areas frequented by males and females. One factor that may be important in this regard is the tree species present in the strata in which each sex does most of its foraging. Holmes and Robinson (1981) showed that birds at Hubbard Brook preferentially seek prey among the foliage of particular plant species. As some of these plant species are confined to or more abundant in particular strata, this may lead to differential foraging by height-separated male and female passerines. Examples at Hubbard Brook are the use of shrub-layer plant species, such as hobblebush and ferns, as foraging substrates by low-foraging female Black-throated Blue Warblers (Table 4) and the greater use of ash and yellow birch foliage, which occurs most abundantly in the upper canopy, by high-foraging female Philadelphia Vireos (Tables 2–4). Similar height-related differences in plant species use were noted by Franzreb (1983) for foraging male and female Yellow-rumped Warblers (*D. coronata*).

Another factor that might influence the foraging heights of male and female passerines is the presence and activity of predators. In some years at Hubbard Brook, chipmunks (*Tamias striatus*), Blue Jays (*Cyanocitta*

*cristata*), and Sharp-shinned Hawks (*Accipiter striatus*) have been more abundant, and have significantly influenced the nesting success of birds (R. T. Holmes and T. W. Sherry, unpubl. data). In years when predators are abundant, their activity may influence the heights and locations of nests, which could, in turn, affect where birds forage.

Differences in the ways these male and female passerine birds exploit their food resources can therefore best be explained by height-related breeding activities. The extent to which these differences are genetically determined or learned is not known. A recent manipulative study by Peters and Grubb (1983), however, demonstrated experimentally that differences in foraging between male and female Downy Woodpeckers (*Picoides pubescens*) in winter were due to females actively avoiding the foraging microhabitats used by dominant males. Similar experimental and field studies would help clarify how labile or fixed these sexual differences in foraging are among forest passerines.

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# THE STRUCTURE OF A FOREST BIRD COMMUNITY DURING WINTER AND SUMMER

MICHAEL L. MORRISON, KIMBERLY A. WITH, AND IRENE C. TIMOSSI[1]

ABSTRACT.—We examined the abundance and use of habitat by birds during winter and summer in a mixed-conifer forest of the western Sierra Nevada. Of the species present during both seasons, four had significantly higher indices of abundance in winter, whereas none had higher summer indices. Bird species differed significantly in habitat use during summer as identified by discriminant function analysis (DFA). The spacing of large trees separated birds along the first DFA axis; the second axis was defined by the size of foraging trees. There was also a significant difference in habitat use among species during winter. The size of foraging trees and the diameter of small (11–30 cm dbh) trees defined the first function; the second function was defined by high canopy cover. In both seasons, however, an unbiased classification procedure separated all species poorly. There was a significant difference in the overall pattern of habitat use by permanent resident birds between winter and summer as identified by DFA. All species showed significant differences in habitat use vs habitat availability during both winter and summer. Overwintering birds used areas characterized by high, heavy canopy cover and heavy subcanopy cover relative to summer use. Our results suggest that forest managers should give increased attention to the structure and species composition of managed forests. *Received 16 Sept. 1985, accepted 22 Nov. 1985.*

Species composition, abundance, and behavior of birds are known to vary seasonally (Willson 1970, 1971; Travis 1977; Conner 1980, 1981; Rice et al. 1980; Hutto 1981; Lewke 1982; Morrison et al. 1985). Some species are permanent residents in an area; others occupy an area only during winter or summer. In addition, the quantity and quality of the habitat, both in terms of plant condition (e.g., leaf abscission) and food resources (e.g., abundance), vary seasonally. The description of the structure of bird communities is thus complicated by many factors.

Our objective was to describe habitat use by birds during winter and summer in the western Sierra Nevada, California; we examined both community and species-specific habitat use. Possible changes in habitat use may indicate a response to environmental differences between seasons, and they are important to recognize if the habitat requirements of birds are to be met by forest managers.

## STUDY AREA

The study was conducted at the Blodgett Forest Research Station (University of California–Berkeley), El Dorado County, California. This 1200-ha forest is in the mixed-conifer zone

[1] Dept. Forestry and Resource Management, Univ. California, Berkeley, California 94720.
[2] (Present address of KAW: Dept. Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011.)

at 1200–1450 m elevation in the western Sierra Nevada. Predominant tree species, in decreasing order of canopy coverage, included incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), and sugar pine (*P. lambertiana*) (Morrison et al., unpubl. data). During the spring and summer (May through August, hereafter referred to as the summer season) of 1983 and 1984, and during winter (November through March) of 1982–83 and 1983–84, four areas totaling about 100 ha (range = 16–35 ha) were used as the study site. Because of limited access to much of Blodgett Forest during winter, we selected areas within the forest that allowed both summer and winter access.

## METHODS

*Bird abundance.*—Sampling points were placed along a preexisting grid used for surveying the forest vegetation for silvicultural purposes. Points ("growth-stocking points") were located about every 120 m along the grid; we randomly selected 40 of these points for counting birds in both winter and summer. All birds seen or heard in a 30-m-radius plot around each point were recorded for 5 min during the first 3 h after sunrise on four occasions each during the summer and winter. Bird abundance was calculated as the mean number of birds recorded per count (=index of abundance). Because many species were sexually monomorphic, data for males and females were combined to determine abundance. Spearman's rank correlation indicated that the relative order of species by abundance was similar ($P < 0.05$) between years within a season, and we combined count data for both years of study in the analysis presented here.

*Habitat use.*—The habitat use by winter, summer, and permanent-resident bird species was recorded. During summer, each area was visited for 2–4 h on 4–5 occasions (at 7–10 day intervals between visits). During winter, each area was visited for about 7 h (total) during a 2–3 day period on 4–6 occasions (at 2–3 week intervals).

Analysis of habitat use was based on the activities of foraging individuals. An observer would walk systematically through an area; when an actively foraging bird was encountered, the substrate (i.e., tree, shrub, ground) the bird was using served as the center of a 10-m-radius plot. Within each plot, a visual estimate of shrub and seedling cover by species and cover of dead and down material by size class (≤10, 11–30, 31–90, and >90 cm diameter) was made. The point-centered quarter method (Mueller-Dombois and Ellenberg 1974:110–115) was used to determine species composition and dbh of trees in 11–30 cm dbh and >30-cm dbh size classes surrounding the foraging substrate. The species and dbh of the foraging tree were also recorded. A randomly oriented 20-m line transect bisecting the center point was used to measure cover by height layers. Presence or absence of live vegetation was noted at each of six heights (1, 4, 10, 20, 30, and 40 m) at 2-m intervals along the transect. Foliage height diversity (FHD; Shannon and Weaver 1949) was calculated. Habitat available to the birds was determined by collecting the same data used to describe bird habitat use at the 40 plots at which birds were counted.

Previous work (Morrison 1984) indicated that a sample of >35 individuals adequately described habitat use. Because we could not obtain this size sample for each species each season, data were combined for the two winters and two summers of our study. Data for males and females were combined for this analysis. Whereas rare species of birds may be important in influencing interspecific relationships in a bird community, they are difficult to analyze because of inadequate sample sizes. Therefore, we examined overall community structure (all species present regardless of sample size) separately for winter and summer, but restricted more detailed statistical treatments to species with adequate samples. Given the problems associated with violations of assumptions and related sample size problems

TABLE 1
ABSOLUTE TREE DENSITY ON STUDY PLOTS AT BLODGETT FOREST RESEARCH STATION, CALIFORNIA

| Species | No. trees per 100 m² | | Total |
|---|---|---|---|
| | 11–30 cm dbh | >30 cm dbh | |
| Incense cedar | 0.72 | 0.44 | 1.16 |
| White fir | 0.37 | 0.39 | 0.76 |
| Douglas-fir | 0.25 | 0.23 | 0.48 |
| Ponderosa pine | 0.06 | 0.20 | 0.26 |
| Sugar pine | 0.02 | 0.13 | 0.15 |
| Black oak | 0.00 | 0.07 | 0.07 |
| Other | 0.06 | 0.03 | 0.09 |
| Total | 1.48 | 1.49 | 2.97 |

in the use and interpretation of multivariate analysis (Johnson 1981, Noon 1981, Morrison 1984), such a procedure is preferable to one ignoring such concerns and reporting questionable results. All analyses were run using the SPSSX computer package (SPSS 1983).

Data were analyzed using discriminant function analysis (DFA) with stepwise inclusion of variables. Standardized discriminant function coefficients were used to interpret the functions (ecologically); correlations of the discriminant scores with the original variables yielded the same conclusions. Our data seldom met the assumption of equality of variance-covariance matrices. Transformation (e.g., log, arcsine; see Sokal and Rohlf 1969:380–387) of original data did not substantially enhance normality. Most classification procedures conducted using DFA were run after first dividing the data set randomly into two parts: one containing about 70% of the original observations with which the DFA was performed, and the second containing the remaining observations for determination of the ability of the first data set to classify the second (an "unbiased" classification procedure; Norusis 1985: 87–88). Such a procedure was especially important given the nonnormality of many of our data sets. For comparisons with large differences in sample sizes, the DFA was run using a random subset of the group with the large *n*. Mahalanobis' distances were calculated to examine all pairwise comparisons between species in habitat use.

Correlation coefficients were calculated for all combinations of original variables. When correlations exceeded 0.5, the variable with the least discriminating power (based on analysis of variance) among species was removed from subsequent analysis. Variables created from combinations of other variables (e.g., total vegetation cover) were not used in any multivariate analysis; FHD was not included in these analyses because of high intercorrelations and low discriminating power relative to other (cover) variables.

## RESULTS

### Vegetation Availability

About one-half of the trees in the 11–30-cm dbh size category (SMDBH) were incense cedar (Table 1). White fir and Douglas-fir, with one-half to one-third the density of cedar, were the only other tree species with densities over 0.1 trees/100 m² in this size range (Table 1). Cedar and white

TABLE 2
AVAILABILITY OF HABITAT MEASURED IN 40 PLOTS AT THE BLODGETT FOREST RESEARCH STATION, CALIFORNIA

| Variable | Mnemonic | $\bar{x}$ | SD |
|---|---|---|---|
| Percent cover of down material (cm diameter) | | | |
| ≤10 | DWN1 | 16.3 | 13.7 |
| 11–30 | DWN2 | 4.0 | 5.4 |
| 31–90 | DWN3 | 1.7 | 2.4 |
| >90 | DWN4 | 0.1 | 0.5 |
| Total | | 22.1 | 17.2 |
| Percent cover by height (m) | | | |
| 1.0 | CVR1 | 17.3 | 23.7 |
| 4.0 | CVR2 | 15.0 | 17.0 |
| 10.0 | CVR3 | 29.8 | 22.7 |
| 20.0 | CVR4 | 36.8 | 23.3 |
| 30.0 | CVR5 | 23.6 | 28.4 |
| 40.0 | CVR6 | 3.4 | 8.3 |
| Total | | 125.9 | 54.5 |
| Tree distribution (m) | | | |
| 11–30 cm dbh | SMDIST | 5.4 | 1.7 |
| >30 cm dbh | LGDIST | 6.3 | 2.3 |
| Tree dbh (m) | | | |
| 11–30 cm dbh | SMDBH | 19.3 | 3.7 |
| >30 cm dbh | LGDBH | 55.0 | 11.3 |

fir were roughly codominant in the larger (>30 cm dbh; LGDBH) size class. Ponderosa pine and Douglas-fir were about one-half as abundant as cedar and fir; sugar pine and black oak were present but in low density.

Total cover of down material was only about 22%; most of this was branches and twigs (<10 cm diameter; DWN1) (Table 2). The forest canopy extended to between 30–40 m in height. The densest cover was at 10 m and 20 m, although cover at all heights under 40 m exceeded 15%. The distribution of small (11–30 cm dbh) and large (>30 cm dbh) trees was about equal. The mean dbh of the smaller size category of trees approached 20 cm, whereas trees in the larger category averaged 55 cm dbh.

## Bird Abundance

Thirty-five species were considered resident in the study area during summer. Only eight of these had indices of abundance over 0.4; the

majority (24 or 69%) had indices less than 0.4 (Table 3). The Dark-eyed Junco (scientific names of birds are in Table 3) and Hermit Warbler were the only species with indices over 1.0.

Twenty-one species were resident during winter. Seven had indices of abundance greater than or equal to 0.4, and 10 had indices greater than or equal to 0.2 (Table 3). The remaining 11 species had indices under 0.2. The American Robin and Golden-crowned Kinglet were the only species with indices over 1.0, although the Red-breasted Nuthatch had an index of 0.99.

Of the species present in both winter and summer, four had significantly higher indices of abundance in winter than in summer; none had significantly higher summer indices (Table 3). The American Robin had a winter abundance about four times greater than its summer abundance; the Chestnut-backed Chickadee, Golden-crowned Kinglet, and Red-breasted Nuthatch had winter abundances about twice that of their summer abundances.

## Bird Habitat Use

*Summer residents.*—There was an overall significant difference in habitat use among bird species during summer as identified by discriminant function analysis (Table 4). Three functions accounted for 100% of the explainable variation in our data set. The spacing of large trees (LGDIST) separated species along the first DFA axis (Fig. 1). The Pileated Woodpecker was associated with areas with relatively closely spaced large trees; the Dusky Flycatcher was found in areas with relatively widely spaced large trees. The remaining species were located between these two extremes.

The second axis was defined by size of foraging trees (FGDBH) used. This axis was influenced most drastically by the Pileated Woodpecker and the Golden-crowned Kinglet, which used the largest and smallest trees for foraging, respectively. The kinglet was, however, barely separated from the remaining species. The two-dimensional graph (Fig. 1) showed that most species were located near the center of the plot. Only 67 of the 190 (35%) pairwise comparisons (Mahalanobis' distances) between species were significant (Table 5). The Pileated Woodpecker and Dusky Flycatcher were significantly separated from all other species (and accounted for over one-half of the significant comparisons). The Mountain Chickadee, Purple Finch, and Black-headed Grosbeak were also significantly different from most of the other species (Table 5).

The unbiased classification analyses separated all species poorly, showing only 10% correct classification. For species on extremes of the axes,

TABLE 3

INDICES OF ABUNDANCE OF BIRDS RECORDED DURING WINTER AND SUMMER AT THE BLODGETT FOREST RESEARCH STATION, CALIFORNIA

| Species | Summer $\bar{x} \pm$ SD | Winter $\bar{x} \pm$ SD |
|---|---|---|
| Red-breasted Sapsucker (*Sphyrapicus ruber*) | 0.34 ± 0.36 | 0 |
| Downy Woodpecker (*Picoides pubescens*) | 0.17 ± 0.53 | 0.09 ± 0.37 |
| Hairy Woodpecker (*P. villosus*) | 0.13 ± 0.29 | 0.19 ± 0.22 |
| White-headed Woodpecker (*P. albolarvatus*) | 0.08 ± 0.26 | 0.17 ± 0.29 |
| Northern Flicker (*Colaptes auratus*) | 0.09 ± 0.24 | 0.11 ± 0.26 |
| Pileated Woodpecker (*Dryocopus pileatus*) | 0.17 ± 0.38 | 0.08 ± 0.23 |
| Olive-sided Flycatcher (*Contopus borealis*) | 0.11 ± 0.32 | 0 |
| Western Wood-Pewee (*C. sordidulus*) | 0.11 ± 0.27 | 0 |
| Hammond's Flycatcher (*Empidonax hammondii*) | 0.44 ± 0.30 | 0 |
| Dusky Flycatcher (*E. oberholseri*) | 0.27 ± 0.34 | 0 |
| Steller's Jay (*Cyanocitta stelleri*) | 0.33 ± 0.56 | 0.21 ± 0.39 |
| Mountain Chickadee (*Parus gambeli*) | 0.34 ± 0.38 | 0.46 ± 0.69 |
| Chestnut-backed Chickadee (*P. rufescens*) | 0.35 ± 0.56 | 0.74 ± 0.51[a] |
| Red-breasted Nuthatch (*Sitta canadensis*) | 0.38 ± 0.36 | 0.99 ± 0.42[b] |
| Brown Creeper (*Certhia americana*) | 0.30 ± 0.46 | 0.34 ± 0.65 |
| Winter Wren (*Troglodytes troglodytes*) | 0.30 ± 0.49 | 0.38 ± 0.26 |
| Golden-crowned Kinglet (*Regulus satrapa*) | 0.86 ± 0.36 | 1.60 ± 0.99[b] |
| Ruby-crowned Kinglet (*R. calendula*) | 0 | 0.19 ± 0.32 |
| Western Bluebird (*Sialia mexicana*) | 0 | 0.10 ± 0.40 |
| Townsend's Solitaire (*Myadestes townsendi*) | 0.08 ± 0.27 | 0.14 ± 0.47 |
| Hermit Thrush (*Catharus guttatus*) | 0.14 ± 0.29 | 0 |
| American Robin (*Turdus migratorius*) | 0.35 ± 0.20 | 1.68 ± 0.56[c] |
| Varied Thrush (*Ixoreus naevius*) | 0 | 0.17 ± 0.45 |
| Solitary Vireo (*Vireo solitarius*) | 0.61 ± 0.20 | 0 |
| Warbling Vireo (*V. gilvus*) | 0.80 ± 0.21 | 0 |
| Nashville Warbler (*Vermivora ruficapilla*) | 0.30 ± 0.32 | 0 |
| Yellow-rumped Warbler (*Dendroica coronata*) | 0.35 ± 0.40 | 0.18 ± 0.43 |
| Hermit Warbler (*D. occidentalis*) | 1.01 ± 0.13 | 0 |
| MacGillivray's Warbler (*Oporornis tolmiei*) | 0.24 ± 0.22 | 0 |
| Western Tanager (*Piranga ludoviciana*) | 0.62 ± 0.22 | 0 |
| Black-headed Grosbeak (*Pheucticus melanocephalus*) | 0.40 ± 0.29 | 0 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 0.14 ± 0.26 | 0.86 ± 2.58 |
| Fox Sparrow (*Passerella iliaca*) | 0.15 ± 0.25 | 0 |
| Dark-eyed Junco (*Junco hyemalis*) | 1.05 ± 0.18 | 0.89 ± 1.10 |
| Brown-headed Cowbird (*Molothrus ater*) | 0.17 ± 0.36 | 0 |
| Purple Finch (*Carpodacus purpureus*) | 0.21 ± 0.27 | 0.10 ± 0.32 |
| Pine Siskin (*Carduelis pinus*) | 0.19 ± 0.52 | 0 |
| Evening Grosbeak (*Coccothraustes vespertinus*) | 0.22 ± 0.45 | 0 |

[a] $P < 0.05$ of a seasonal difference using a *t*-test.
[b] $P < 0.01$ of a seasonal difference using a *t*-test.
[c] $P < 0.001$ of a seasonal difference using a *t*-test.

TABLE 4

HABITAT USED BY BIRDS DURING WINTER AND SUMMER, AND A COMPARISON OF WINTER VS SUMMER (ALL BIRD SPECIES COMBINED PER SEASON) AT THE BLODGETT FOREST RESEARCH STATION, CALIFORNIA, AS ANALYZED BY DISCRIMINANT FUNCTION ANALYSIS

| | Winter[a] | | Summer[b] | | | Winter vs summer[c] |
|---|---|---|---|---|---|---|
| | I | II | I | II | III | I |
| Eigenvalue | 0.126 | 0.051 | 0.324 | 0.275 | 0.153 | 0.474 |
| Relative % variation | 61.5 | 25.1 | 43.1 | 36.7 | 20.3 | 100.0 |
| Cumulative % variation | 61.5 | 86.6[d] | 43.1 | 79.7 | 100.0 | 100.0 |
| Canonical correlation | 0.335 | 0.221 | 0.494 | 0.465 | 0.364 | 0.567 |
| Wilks' lambda | 0.822 | 0.926 | 0.514 | 0.680 | 0.868 | 0.678 |
| $\chi^2$ | 72.535 | 28.566 | 156.76 | 90.74 | 33.44 | 112.76 |
| df | 27 | 16 | 57 | 36 | 17 | 5 |
| $P$ | <0.001 | <0.05 | <0.001 | <0.001 | <0.01 | <0.001 |

[a] Box's M: F = 1.47; df = 54, 17,833.6; $P < 0.05$.
[b] Box's M: F = 1.93; df = 114, 10,057.2; $P < 0.001$.
[c] Box's M: F = 3.43; df = 15, 256,880.8; $P < 0.001$. Winter N = 266, which represents a random subsample of 511 plots. This subsample was taken to approximate more closely the summer sample of 181.
[d] The third function accounted for the remaining 13.4% of the variation but was nonsignificant ($P < 0.2$).

the percent classification was above average: 100% for the Pileated Woodpecker, 40% for the Dusky Flycatcher, and 25% for the grosbeak; no kinglets were correctly classified, however.

*Winter residents.*—There was a significant difference in habitat use among species during winter as identified by DFA (Table 4). Two functions were significant and accounted for most of the explainable variation in the data set. The diameter of foraging trees and the diameter of the small size class of trees defined the first function. Except for the Pileated Woodpecker, which used areas typified by large foraging trees and the largest of the smaller size class of trees, little obvious separation was noted along the first axis (Fig. 2).

The second function was defined by high canopy cover (CVR5). Here again, little separation was noted among species except for the Pileated and Hairy woodpeckers. The Hairy Woodpecker tended to use areas with heavy canopy cover, and the Pileated Woodpecker used areas with low canopy cover.

About one-half (25 or 56%) of the 45 pairwise comparisons between species were significant (Table 5). The Pileated Woodpecker, Ruby-crowned Kinglet, and Dark-eyed Junco were significantly separated from all or nearly all of the other species. The generally poor separation among species

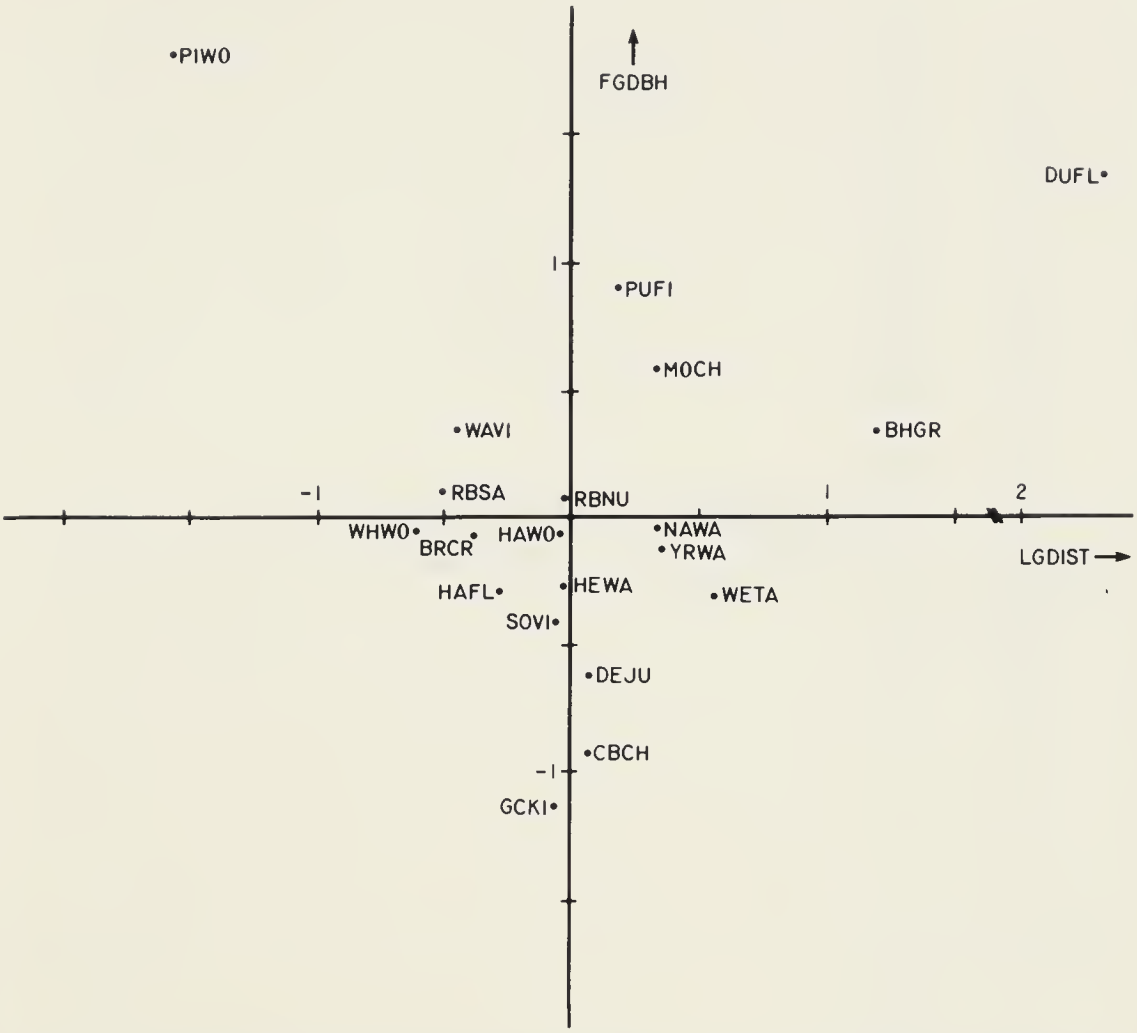


FIG. 1. Two-dimensional ordination of bird habitat use during summer at Blodgett Forest, California, as determined by discriminant function analysis. The species and their associated mnemonics and sample sizes are given in Appendix 1. See Table 4 for statistics associated with this analysis. Variables defining the axes are FGDBH (dbh of the foraging tree) and LGDIST (distribution of large trees).

was reflected in the unbiased classification; only 14% were correctly classified. The two species on the extremes of the axes did show correct classification rates higher than average (100% for the pileated and 22% for the hairy).

*Permanent residents, winter vs summer.*—There was a significant difference in the overall pattern of habitat use by permanent resident birds between winter (all species combined) and summer (all species combined) as identified by DFA (Table 4). There was a greater use of high cover and more widely scattered large trees during winter. Use of cover in the second (CVR2) layer was also greater during winter. The overall use of larger diameter trees was greater during summer. The discriminant analysis was fairly strong, showing an unbiased classification of 69%.

TABLE 5

SIGNIFICANCE[a] BETWEEN PAIRS OF SPECIES AS DETERMINED BY MAHALANOBIS' DISTANCE (ASSOCIATED WITH DISCRIMINANT FUNCTION ANALYSIS) (TABLE 4) FOR BIRD HABITAT USE AT BLODGETT FOREST, CALIFORNIA, DURING SUMMER (LOWER-LEFT TRIANGLE) AND WINTER (UPPER-RIGHT TRIANGLE)

| | RBSA[b] | HAWO[c] | WHWO[c] | PIWO[c] | HAFL | DUFL | MOCH[c] | CBCH[c] | RBNU[c] | BRCR[c] | GCKI[c] | RCKI[c] | SOVI | WAVI | NAWA | YRWA | HEWA | WETA | BHGR | DEJU[c] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HAWO[c] | | — | | * | * | | | | * | | | | | | | | | | | * |
| WHWO[c] | | | — | * | | | | | | | | * | | | | | | | | * |
| PIWO[c] | * | * | * | — | | | * | | * | * | * | * | | | | | | | | * |
| HAFL | | | | * | — | | | | | | | | | | | | | | | |
| DUFL | * | * | * | * | * | — | | | | | | | | | | | | | | |
| MOCH[c] | | | * | * | * | * | — | * | * | | | * | | | | | | | | |
| CBCH[c] | | | | * | | * | * | — | | * | | * | | | | | | | | * |
| RBNU[c] | | | | * | | * | | | — | * | * | * | | | | | | | | * |
| BRCR[c] | | | | * | | * | * | | | — | | * | | | | | | | | |
| GCKI[c] | | | | * | | * | * | | | | — | * | | | | | | | | |
| RCKI[c] | | | | | | | | | | | | — | | | | | | | | |
| SOVI | | | | * | | * | * | | | | | | — | | | | | | | |
| WAVI | | | | * | | * | | | | | | | | — | | | | | | |
| NAWA | | | | * | * | * | | | | | * | | | | — | | | | | |
| YRWA | | | | * | | * | | | | | | | | | | — | | | | |
| HEWA | | | | * | | * | | | | | | | | | | | — | | | |
| WETA | | | | * | | * | | | | | | | | | | | | — | | |
| BHGR | | | * | * | * | * | | * | | * | * | | * | * | | | | | — | |
| DEJU[c] | | | | * | | * | * | | | | | | | | | | | | * | — |
| PUFI | * | | * | * | * | * | * | * | * | * | * | | * | | * | * | * | | * | |

[a] $P < 0.05$.
[b] See Appendix 1 for species abbreviations.
[c] Species present during winter.

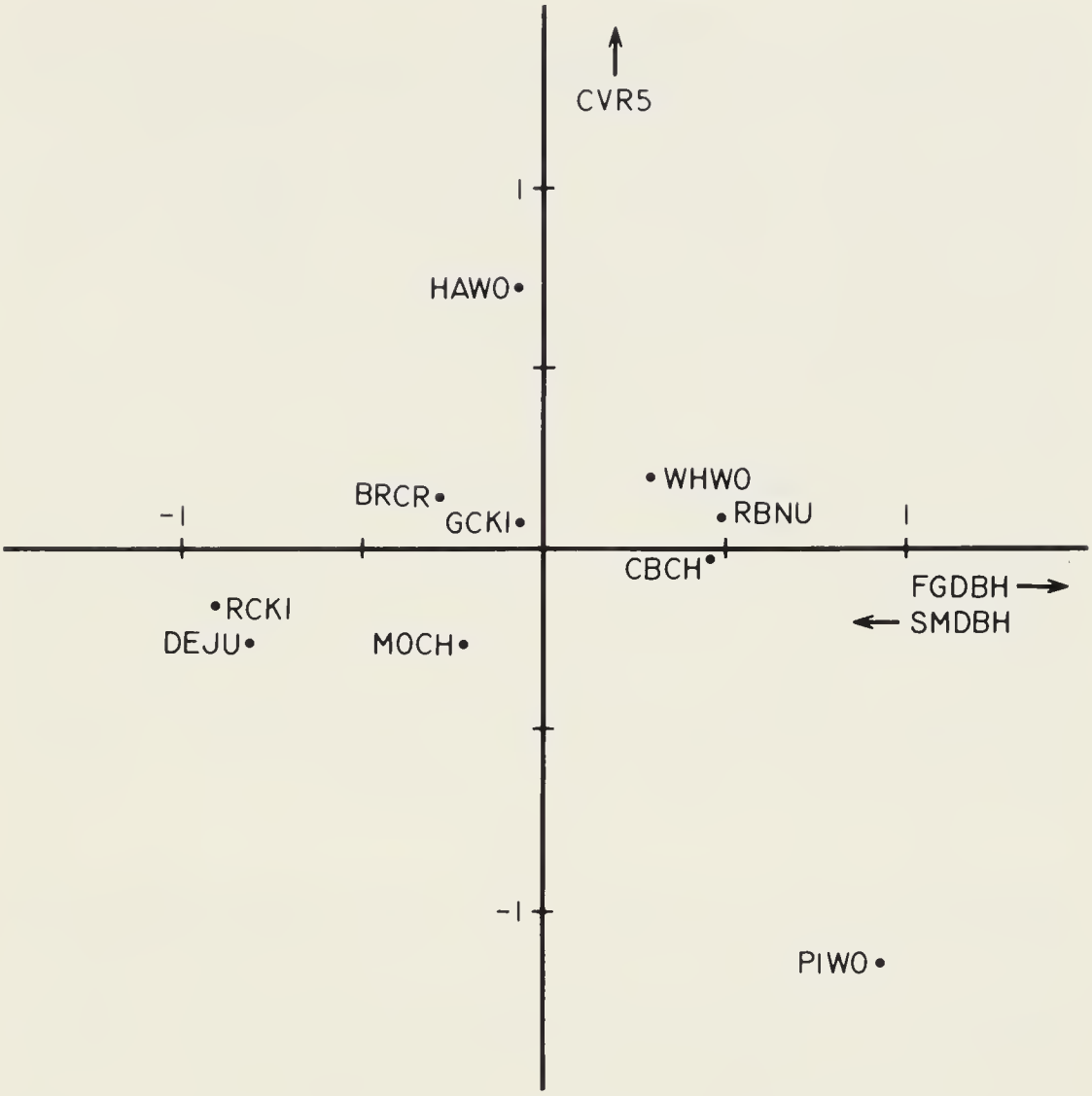


FIG. 2. Two-dimensional ordination of bird habitat use during winter at Blodgett Forest, California, as determined by discriminant function analysis. The species and their associated mnemonics (except for the Ruby-crowned Kinglet, RCKI) and sample sizes are given in Appendix 1. See Table 4 for statistics associated with this analysis. Variables defining the axes are CVR5 (canopy cover), FGDBH (dbh of the foraging tree), and SMDBH (dbh of the small size class of trees).

All permanent resident species analyzed used areas typified by greater use of high (canopy) cover or widely scattered large trees in winter versus summer, except for the Golden-crowned Kinglet, which showed no significant differences between seasons (Appendix 1). The White-headed Woodpecker and Mountain Chickadee also used smaller foraging trees during winter; low (subcanopy) cover was also of higher use in winter by the nuthatch.

*Species-specific habitat use vs availability: summer.*—All 20 species analyzed showed significant differences between habitat use and habitat avail-

ability during summer (Appendix 1). Only 11, however, showed greater than 70% correct unbiased classification; an additional four species showed over 60% unbiased classification. The diameter of the foraging tree was the primary variable separating summer habitat use from availability for 15 species, with these species using larger trees for foraging in proportion to those available randomly (Appendix 1). The distribution of large diameter or small diameter trees separated the remaining species, except for the Dark-eyed Junco and Black-headed Grosbeak.

*Species-specific habitat use vs availability: winter.*—All nine species analyzed during winter showed significant differences between habitat use and availability (Appendix 1). Four showed over 70% correct unbiased classification; the remaining five species had classification rates from 55% to 69%. All species except the Pileated Woodpecker used greater cover in the second, third, or fifth height layer relative to that available randomly as either the primary, secondary, or tertiary variable separating use from availability of habitat. The Chestnut-backed Chickadee and Pileated Woodpecker used significantly larger trees for foraging than those available randomly, and the Hairy Woodpecker used areas with smaller diameter trees relative to those available randomly.

## DISCUSSION

Blodgett Forest is a true mixed-coniferous forest; all predominant tree species can usually be seen at any point in the forest. The subcanopy and canopy layers were similar in foliage cover up to 30–40 m in height, and the distribution of trees in both size classes was similar. This structure of the forest vegetation may account for our finding that most species had similar abundance—low to moderate—relative to the two or three species with the highest abundances (during either season). It thus appeared that the forest vegetation offered adequate habitat for many species, but few species were able to attain relatively high abundance. This supposition is supported by results of analysis of habitat use. Except for the Pileated Woodpecker, little obvious separation was seen among species on the discriminant plots during either season, using the variables we measured.

More species were considered resident during summer than winter (35 vs 21). Of the year-round residents, four species had higher abundances in winter than summer, whereas none had higher abundances in summer than winter. This could result from a change in the detectability of a species between seasons; interpretation of the indices is hampered because many species formed interspecific foraging flocks during winter. If our results reflect actual shifts in abundance, it appears that while relatively few species overwinter in our study area, those that do, do so at higher numbers than in the summer.

The bird community overwintering at Blodgett used areas characterized by high, heavy canopy cover provided by large, widely spaced trees; heavier cover in the subcanopy was also used during winter compared to summer. We attributed this difference in habitat use to the protection from wind and precipitation supplied by relatively large trees with dense canopies that formed an "umbrella" over the forest floor and the denser subcanopy that further protected the birds from adverse weather (i.e., thermal cover; see Thomas et al. 1979; also Kittredge 1953, Gary and Troendle 1982). Although we do not have adequate data to present an energetics model, others have shown that such habitat is preferred by numerous species of animals in an attempt to escape inclement weather (see reviews by Moen 1973:286–292, Thomas et al. 1979).

Morrison et al. (1985) showed that the use of trees with smaller diameters for foraging during winter at Blodgett Forest was primarily a reflection of the use of small incense cedar. Birds increased use of cedar because of the presence of a readily accessible insect (incense cedar scale, *Xylococculus macrocarpae*) overwintering just under the loose bark of small trees. The presence of this food source may explain the higher winter abundance of certain species shown in this paper.

Species-specific analysis of habitat use (vs availability) generally paralleled results for our community-level analyses—larger diameter trees were used for foraging in summer and areas with high canopy cover at one or more heights were used in winter. During summer, birds apparently were using relatively large trees as singing and foraging sites—our data were often collected on individuals alternately singing and foraging in large trees. During winter, when song perches were not usually used, thermal protection became important and small cedars apparently were preferred.

Our results suggest a word of caution to forest managers. In the western Sierra Nevada (and elsewhere), forests are being managed for preferred commercial species (e.g., Douglas-fir, ponderosa pine, fir) and short (e.g., 70 years) rotation. Therefore, the habitat conditions used by birds during winter in our study—dense canopy with an understory of young incense cedar—are being replaced by relatively monotypic stands of younger trees. Although our results are descriptive and not predictive, it is apparent that more attention needs to be given to the structure and species composition of managed forests.

ACKNOWLEDGMENTS

We thank P. N. Manley, W. M. Block, K. A. Milne, S. A. Laymon, R. Etemad, and J. M. Anderson, for assisting with data collection during part of the study, and L. B. Best, R. W. Mannan, R. N. Conner, and an anonymous referee for reviewing an earlier draft. We especially thank R. C. Heald for assistance with logistics at Blodgett Forest.

## Appendix 1

Summary of Discriminant Function Analysis (DFA) of Habitat Use vs Habitat Availability (N = 40 plots), and Winter vs Summer Habitat Use, for Birds at Blodgett Forest Research Station, California, during Summer and Winter[a]

| | Summer use vs availability | | | | | Winter use vs availability | |
|---|---|---|---|---|---|---|---|
| | DFA (*P*) (N) | Standardized discriminant function coefficients | | | % Classification | DFA (*P*) (N) | Standardized discriminant function coefficients |
| Red-breasted Sapsucker (RBSA) | <0.001 (20) | FGDBH (0.741) | CVR2 (0.656) | LGDIST (−0.511) | 77.8 | | |
| Hairy Woodpecker (HAWO) | <0.001 (18) | FGDBH (1.000) | | | 72.2 | <0.001 (28) | LGDBH (−0.945) |
| White-headed Woodpecker (WHWO) | <0.001 (20) | FGDBH (0.916) | CVR3 (0.622) | SMDBH (−0.530) | 76.5 | <0.05 (35) | CVR2 (1.000) |
| Pileated Woodpecker (PIWO) | <0.001 (15) | FGDBH (1.000) | | | 95.0 | <0.001 (12) | FGDBH (0.900) |
| Hammond's Flycatcher (HAFL) | <0.001 (29) | FGDBH (0.560) | CVR3 (0.476) | LGDIST (−0.716) | 63.6 | | |
| Dusky Flycatcher (DUFL) | <0.01 (10) | SMDIST (0.754) | LGDIST (0.767) | | 75.0 | | |
| Mountain Chickadee (MOCH) | <0.001 (21) | FGDBH (0.925) | CVR2 (0.758) | LGDBH (−0.670) | 68.4 | <0.001 (58) | CVR2 (0.661) |
| Chestnut-backed Chickadee (CBCH) | <0.001 (19) | SMDIST (0.644) | LGDIST (0.754) | | 80.0 | <0.001 (38) | FGDBH (0.824) |
| Red-breasted Nuthatch (RBNU) | <0.01 (27) | FGDBH (0.712) | LGDIST (−0.620) | | 50.0 | <0.001 (79)[b] | SMDBH (−0.574) |
| Brown Creeper (BRCR) | <0.001 (23) | FGDBH (0.755) | LGDIST (−0.672) | | 72.2 | <0.001 (69) | CVR2 (0.761) |

## Appendix 1
Continued

| | Summer use vs availability | | | | | Winter use vs availability | |
|---|---|---|---|---|---|---|---|
| | DFA (*P*) (N) | Standardized discriminant function coefficients | | | % Classification | DFA (*P*) (N) | Standardized discriminant function coefficients |
| Golden-crowned Kinglet (GCKI) | <0.001 (12) | FGDBH (0.878) | CVR2 (−0.592) | LGDIST (0.565) | 73.7 | <0.001 (55)[c] | CVR3 (0.579) |
| Solitary Vireo (SOVI) | <0.05 (21) | FGDBH (0.585) | SMDIST (−0.565) | LGDIST (−0.704) | 50.0 | | |
| Warbling Vireo (WAVI) | <0.05 (14) | LGDIST (1.000) | | | 36.8 | | |
| Nashville Warbler (NAWA) | <0.001 (13) | FGDBH (1.236) | DWN3 (0.797) | LGDBH (−0.671) | 68.8 | | |
| Yellow-rumped Warbler (YRWA) | <0.01 (25) | FGDBH (1.066) | DWN3 (0.785) | LGDBH (−0.760) | 75.0 | | |
| Hermit Warbler (HEWA) | <0.001 (21) | FGDBH (0.637) | CVR3 (0.646) | LGDIST (−0.588) | 70.0 | | |
| Western Tanager (WETA) | <0.05 (12) | FGDBH (1.000) | | | 68.8 | | |
| Black-headed Grosbeak (BHGR) | <0.01 (13) | DWN3 (1.000) | | | 52.6 | | |
| Dark-eyed Junco (DEJU) | <0.01 (13) | CVR2 (−0.687) | LGDIST (0.807) | | 52.2 | <0.001 (19) | CVR2 (0.881) |
| Purple Finch (PUFI) | <0.05 (13) | FGDBH (1.000) | | | 75.0 | | |

[a] Mnemonics given in Table 2 (FGDBH = dbh of foraging tree).
[b] Represents a subsample of 125 plots.
[c] Represents a subsample of 127 plots.

## Appendix 1
Continued

| | Winter use vs availability | | | Winter vs summer use | | | | |
|---|---|---|---|---|---|---|---|---|
| | Standardized discriminant function coefficients | | % Classification | DFA (*P*) | Standardized discriminant function coefficient | | | % Classification |
| Red-breasted Sapsucker (RBSA) | | | | | | | | |
| Hairy Woodpecker (HAWO) | CVR5 (0.836) | CVR2 (0.626) | 55.2 | <0.05 | CVR5 (1.000) | | | 80.0 |
| White-headed Woodpecker (WHWO) | | | 56.0 | <0.01 | CVR5 (0.805) | FGDBH (−0.718) | | 41.7 |
| Pileated Woodpecker (PIWO) | LGDBH (−0.568) | | 85.0 | <0.05 | LGDIST (1.000) | | | 100.0 |
| Hammond's Flycatcher (HAFL) | | | | | | | | |
| Dusky Flycatcher (DUFL) | | | | | | | | |
| Mountain Chickadee (MOCH) | CVR3 (0.542) | FGDBH (0.528) | 75.9 | <0.001 | CVR5 (0.918) | FGDBH (−0.797) | | 55.6 |
| Chestnut-backed Chickadee (CBCH) | CVR2 (0.849) | | 83.9 | <0.001 | LGDIST (0.853) | CVR5 (0.797) | | 58.3 |
| Red-breasted Nuthatch (RBNU) | CVR5 (0.488) | CVR2 (0.462) | 87.8 | <0.001 | SMDBH (−0.679) | CVR5 (0.500) | CVR2 (0.463) | 80.5 |
| Brown Creeper (BRCR) | CVR3 (0.516) | LGDIST (−0.566) | 67.6 | <0.001 | LGDBH (−0.862) | LGDIST (0.842) | CVR5 (0.608) | 54.6 |
| Golden-crowned Kinglet (GCKI) | SMDBH (−0.504) | SMDIST (−0.481) | 64.0 | >0.05 | | | | |

## Appendix 1
Continued

| | Winter use vs availability | | Winter vs summer use | | | |
|---|---|---|---|---|---|---|
| | Standardized discriminant function coefficients | % Classification | DFA (*P*) | Standardized discriminant function coefficient | | % Classification |
| Solitary Vireo (SOVI) | | | | | | |
| Warbling Vireo (WAVI) | | | | | | |
| Nashville Warbler (NAWA) | | | | | | |
| Yellow-rumped Warbler (YRWA) | | | | | | |
| Hermit Warbler (HEWA) | | | | | | |
| Western Tanager (WETA) | | | | | | |
| Black-headed Grosbeak (BHGR) | | | | | | |
| Dark-eyed Junco (DEJU) | LGDBH (−0.497) | 69.6 | <0.01 | LGDIST (0.750) | CVR5 (0.841) | 75.0 |
| Purple Finch (PFUI) | | | | | | |

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# NEST-SITE CHARACTERISTICS OF OPEN-NESTING BIRDS IN RIPARIAN HABITATS IN IOWA

DEAN F. STAUFFER AND LOUIS B. BEST[1]

ABSTRACT.—We analyzed interrelationships among nest sites of 13 open-nesting bird species of riparian communities in Iowa. Cluster analysis of a Euclidean distance matrix, based on the nesting substrate and mean values of nest-site measurements, identified three nesting assemblages comprising species nesting primarily in trees (six species), shrubs (four), or herbaceous cover (three). Discriminant canonical analyses were used to elucidate relationships among species within each nesting group. Two canonical axes separated most species nesting in trees along gradients of (I) nest and support-structure height and (II) support-limb diameter, distance to periphery of substrate, and nest height. Nest sites of American Robins (*Turdus migratorius*) were not different ($P > 0.05$) from those of Blue Jays (*Cyanocitta cristata*) and Mourning Doves (*Zenaida macroura*), which did differ from each other. Two canonical axes, representing (I) nest and support-structure height and (II) support-limb diameter and cover at the nest, separated all shrub-nesting species except Gray Catbirds (*Dumetella carolinensis*) and Brown Thrashers (*Toxostoma rufum*). One significant ($P < 0.05$) canonical axis, representing nest and relative nest height and cover at the nest, separated Red-winged Blackbirds (*Agelaius phoeniceus*) from Common Yellowthroats (*Geothlypis trichas*) and Song Sparrows (*Melospiza melodia*), which did not differ from each other. Species with similar nest sites tended to have different habitat use patterns. Nest-site analysis should be considered when investigating intra-community relationships among birds. *Received 17 Aug. 1985, accepted 26 Dec. 1985.*

Considerable effort has been devoted to investigating interspecies relationships within avian communities, but little research has focused on differences in nest-site use at the community level. Nest-site selection is an integral component of habitat selection and may be influenced by interrelationships among species in avian communities. Beecher (1942) provided the first general description of nest-site characteristics within a community. The heights at which birds nest in various habitats have been reported by several authors (Preston 1946, Preston and Norris 1947, Cruickshank 1956, Taylor 1965, DeGraff et al. 1975), but additional nest-site measurements were not provided. More recently, McCrimmon (1978), Collins (1981), Titus and Mosher (1981), MacKenzie et al. (1982), and Clark et al. (1983) have used multivariate methods to investigate relationships among nest sites.

Our objective was to describe the interrelationships among nest sites used by open-nesting species of riparian communities (herein defined as

[1] Dept. Animal Ecology, Iowa State Univ., Ames, Iowa 50011. (Present Address of DFS: Dept. Fish and Wildl. Sci., Virginia Polytechnic Institute and State Univ., Blacksburg, Virginia 24061.)

TABLE 1

MEANS (SE) OF VARIABLES MEASURED AT 517 OPEN NESTS OF BIRD SPECIES NESTING IN RIPARIAN HABITATS IN IOWA

| | Abbreviated name | N | Nest height (m) | Support-structure height (m) | Relative nest height (%) |
|---|---|---|---|---|---|
| Tree-nesting species | | | | | |
| Mourning Dove (*Zenaida macroura*) | MD | 58 | 2.4 (0.2) A[a] | 6.0 (0.6) A | 47.6 (3.1) A |
| Eastern Wood-Pewee (*Contopus virens*) | EWP | 20 | 8.6 (0.6) B | 17.5 (0.9) B | 49.6 (3.1) AB |
| Blue Jay (*Cyanocitta cristata*) | BJ | 34 | 6.1 (0.7) C | 13.8 (1.1) BC | 44.4 (2.9) A |
| American Robin (*Turdus migratorius*) | AR | 17 | 4.7 (0.9) C | 9.8 (1.3) AC | 49.8 (4.9) AC |
| Northern Oriole (*Icterus galbula*) | NO | 13 | 11.0 (0.9) B | 20.6 (1.9) B | 60.0 (7.0) AD |
| Rose-breasted Grosbeak (*Pheucticus ludovicianus*) | RBG | 47 | 4.2 (0.4) C | 7.3 (0.7) A | 64.3 (2.9) BCD |
| Shrub-nesting species | | | | | |
| Gray Catbird (*Dumetella carolinensis*) | GC | 92 | 1.4 (0.1) A | 2.5 (0.1) A | 56.9 (1.6) A |
| Brown Thrasher (*Toxostoma rufum*) | BT | 31 | 1.2 (0.1) A | 2.7 (0.4) A | 52.7 (2.6) A |
| Northern Cardinal (*Cardinalis cardinalis*) | NC | 74 | 1.4 (0.1) A | 2.7 (0.2) A | 55.1 (2.1) A |
| Indigo Bunting (*Passerina cyanea*) | IB | 41 | 0.6 (0.1) B | 1.2 (0.1) B | 51.0 (2.2) A |
| Herbaceous-nesting species | | | | | |
| Common Yellowthroat (*Geothlypis trichas*) | CY | 12 | 0.1 (0.0) A | 1.2 (0.1) A | 11.3 (1.7) A |
| Red-winged Blackbird (*Agelaius phoeniceus*) | RWB | 31 | 0.6 (0.1) B | 1.2 (0.2) A | 51.7 (2.6) B |
| Song Sparrow (*Melospiza melodia*) | SS | 12 | 0.1 (0.1) A | 0.8 (0.1) A | 11.2 (3.6) A |

[a] Bonferroni *t*-tests; values within each species assemblage with the same capital letter are not significantly different ($P > 0.05$).

[b] Value in brackets indicates sample size if different from that first presented.

TABLE 1
EXTENDED

| Cover | | Support-limb diameter (cm) | Distance to support (m) | |
|---|---|---|---|---|
| Above | Below | | Trunk | Periphery |
| 2.5 (0.1) A | 2.0 (0.1) A | 5.7 (0.9) A | 0.8 (0.1) [48][b] A | 1.7 (0.1) [54] A |
| 2.4 (0.1) A | 1.1 (0.1) A | 3.6 (0.2) A | 3.8 (0.4) B | 1.9 (0.2) A |
| 2.8 (0.1) AB | 1.9 (0.1) A | 8.5 (0.7) B | 1.9 (0.5) [32] A | 2.7 (0.2) A |
| 2.8 (0.2) AC | 2.0 (0.2) A | 7.3 (1.0) AB | 1.6 (0.6) [16] A | 1.8 (0.3) [16] A |
| 3.5 (0.2) BC | 2.3 (0.3) A | 0.7 (0.2) C | 5.0 (0.9) B | 0.8 (0.3) B |
| 3.1 (0.1) BC | 2.1 (0.1) A | 1.6 (0.1) D | 1.2 (0.2) [40] A | 0.9 (0.1) [45] B |
| 3.2 (0.1) A | 3.1 (0.1) A | 1.3 (0.2) A | | |
| 3.4 (0.1) AB | 3.1 (0.1) AB | 1.8 (0.7) A | | |
| 3.1 (0.1) A | 2.8 (0.1) B | 1.0 (0.1) A | | |
| 3.9 (0.1) B | 3.5 (0.1) B | 0.4 (0.1) [24] B | | |
| 3.9 (0.1) A | 4.0 (0.0) A | — | | |
| 2.9 (0.1) B | 3.2 (0.2) [28] B | 1.0 (0.3) [10] | | |
| 3.6 (0.2) A | 4.0 (0.0) A | — | | |

uncultivated land within 250 m of a stream edge). Previously, we have reported on the interrelationships among nest sites of cavity-nesting species (Stauffer and Best 1982).

## STUDY AREA AND METHODS

Twenty-eight sites were selected for study in southeastern Guthrie County, Iowa, along Brushy Creek, Beaver Creek, and the Middle and South Raccoon rivers. In choosing study sites, we attempted to sample a broad spectrum of riparian habitats from open hayfields and pasture to closed-canopy woodlands. Characteristics of the study area and the habitats sampled (142 total ha) are detailed in Stauffer and Best (1980).

Field work was conducted from mid-April through mid-July in 1976 and 1977 as part of a study of the avian community (Stauffer and Best 1980). Some nests were found during early morning bird counts on the study sites, but most were located in the morning after counts and during the evening, when we watched nesting behavior and systematically searched suitable areas. We attempted to locate nests of every open-nesting species on each study site. The sample is biased, however, because less well concealed nests and those located in more open sites, where birds could be followed more easily, were probably represented disproportionately.

For each nest, we recorded nest height and height of the supporting substrate, relative nest height (nest height/support height), diameter of supporting limb(s), cover above and below the nest (1 = poor, 2 = fair, 3 = good, 4 = excellent), distance from nest to trunk and substrate periphery (for nests in trees), and life form of nesting substrate (forb, grass, shrub, deciduous sapling or tree, evergreen tree).

Mean values of the variables for each species were calculated. A matrix of Euclidean distances (Pielou 1984:14) between each species pair was calculated using nest, support-structure, and relative nest heights; support-limb diameter; cover above and below the nest; and percentage of nests in substrates of each life form. (Life-form data are presented in Stauffer and Best 1980.) The Common Yellowthroat (scientific names of species are in Table 1) and Song Sparrow were assigned a support-limb diameter value of 0.3 cm, which is approximately the diameter of herbaceous vegetation typically supporting their nests (diameter measurements were not made on herbaceous vegetation). We then conducted a cluster analysis (BMDP1M, Dixon 1983) on the matrix of pair-wise distance values to develop a dendrogram illustrating the relationships among species on the basis of nest-site characteristics.

For each of the three nesting assemblages identified through cluster analysis, we conducted analyses of variance (ANOVA) to test the null hypothesis of no difference among species for each variable. Bonferroni *t*-tests (Ray 1982) were used for multiple comparisons of differences between pairs of species within each assemblage. Canonical discriminant analyses also were conducted to further determine relationships among the species within each nesting group. Only species represented by at least 12 nests were analyzed. Before statistical analyses, data were checked for normality and, when necessary, were transformed to achieve a more normal distribution.

## RESULTS AND DISCUSSION

Cluster analysis delineated three assemblages of species, represented by those nesting predominantly in tree, shrub, or herbaceous substrates (Fig. 1). Relationships among species within each of these three groups are addressed below.

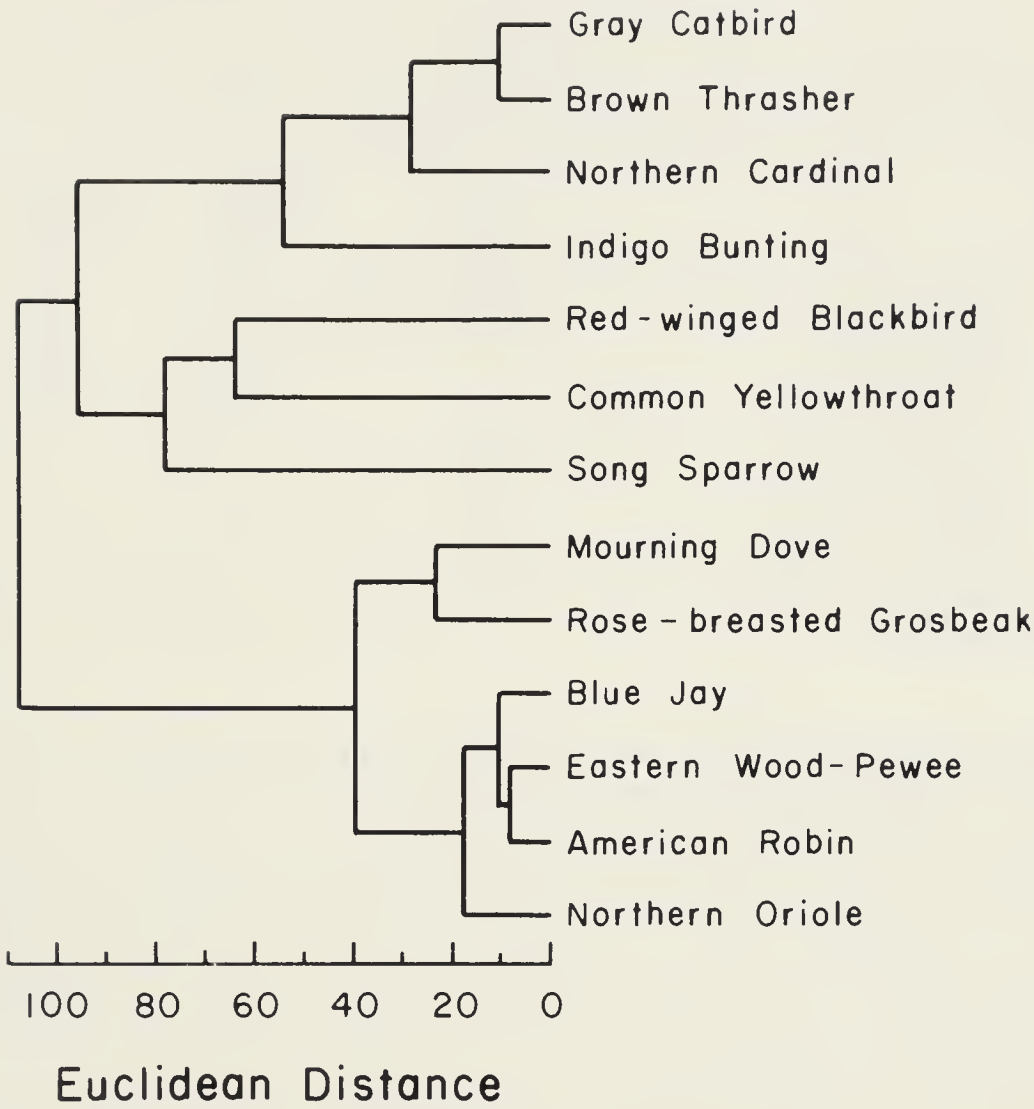


FIG. 1. Dendrogram depicting the relationships among nest sites of 13 open-nesting bird species. Results are based on a cluster analysis of a Euclidean-distance matrix derived from nest-site characteristics.

*Univariate analyses.*—Nest heights differed ($P < 0.05$) among species within each nesting assemblage (Table 2). Nests of tree-nesting species were distributed in three strata, with the Northern Oriole and Eastern Wood-Pewee nesting at the highest level and the Mourning Dove nesting at the lowest level (Table 1) (see also DeGraff et al. 1975). Indigo Buntings nested lower than other species in the shrub-nesting group, and among the herbaceous-nesting species, Red-winged Blackbirds had nests in the highest locations. Nest height was positively related to support-structure height and relative nest height for all nesting groups but negatively correlated with cover above and below the nest; higher nests were less well concealed (Table 3). For shrub- and herbaceous-nesting species, nest height also was correlated with support-limb diameter.

TABLE 2

*F* STATISTICS FROM ONE-WAY ANOVA'S TO TEST THE NULL HYPOTHESES OF NO DIFFERENCE IN NEST-SITE CHARACTERISTICS AMONG SPECIES WITHIN EACH NESTING GROUP

| Variable | Tree-nesting species (df = 5,158) | Shrub-nesting species (df = 3,234) | Herbaceous-nesting species (df = 2,52) |
|---|---|---|---|
| Nest height | 25.87[a] | 27.30[a] | 33.12[a] |
| Support-structure height | 20.81[a] | 20.68[a] | 3.02 |
| Relative nest height | 6.13[a] | 1.57 | 67.34[a] |
| Cover above nest | 5.57[a] | 8.63[a] | 10.89[a] |
| Cover below nest | 5.98[a] | 8.78[a] | 7.23[b] |
| Support-limb diameter | 36.21[a] | 16.78[a] | |
| Distance to trunk | 8.44[a] | | |
| Distance to periphery | 14.69[a] | | |

[a] Indicates $P < 0.001$.
[b] Indicates $P < 0.01$.

Support-structure height followed trends similar to those for nest height (Table 1), and differed among tree-nesting species and among shrub-nesting species (Table 2). The negative correlation of support-structure height with relative nest height for tree and shrub nesters (Table 3) implies that nests were placed relatively lower in taller plants. Within each nesting group, support-limb diameter was positively correlated with support-structure height, indicating that nests were supported by larger limbs in taller substrates (Table 3).

Relative nest height differed for tree- and herbaceous-nesting species but not for shrub nesters (Table 2). Northern Orioles and Rose-breasted Grosbeaks nested relatively higher than some of the other species in the tree-nesting assemblage; Red-winged Blackbirds nested relatively higher than the other two species using herbaceous cover (Table 1). Nests placed relatively higher in trees and shrubs were supported by smaller limbs (Table 3).

Cover above and below the nest differed within all nesting assemblages (Table 2); these two measures were significantly correlated (Table 3). For tree and shrub nesters, cover above the nest was greater than cover below the nest; the opposite was true for species nesting in dense herbaceous vegetation (Table 1). Cover above the nest was negatively related to support-structure height for shrub nesters, and cover below the nest correlated negatively with support-structure height for both shrub- and tree-nesting species (Table 3). Thus, nests placed in taller woody substrates tended to be less well concealed, primarily because nests were placed relatively lower in taller substrates. In contrast, as height of herbaceous substrates in-

TABLE 3

SIGNIFICANT ($P < 0.05$) CORRELATIONS BETWEEN VARIABLES MEASURED AT NEST SITES OF SPECIES IN THE TREE- (N = 189), SHRUB- (N = 238), AND HERBACEOUS- (N = 55) NESTING GROUPS

| | Nesting group | NH[a] | SSH | RNH | CAN | CBN | SLD | DT |
|---|---|---|---|---|---|---|---|---|
| Support-structure height | Tree | 0.83[b] | | | | | | |
| | Shrub | 0.80[b] | | | | | | |
| | Herbaceous | 0.37[b] | | | | | | |
| Relative nest height | Tree | 0.21[b] | −0.34[b] | | | | | |
| | Shrub | 0.40[b] | −0.21[b] | | | | | |
| | Herbaceous | 0.81[b] | | | | | | |
| Cover above nest | Tree | −0.16[c] | | 0.26[b] | | | | |
| | Shrub | −0.19[c] | −0.24[c] | | | | | |
| | Herbaceous | −0.35[c] | | −0.38[b] | | | | |
| Cover below nest | Tree | −0.19[c] | −0.36[b] | 0.33[c] | 0.48[b] | | | |
| | Shrub | −0.27[b] | −0.22[b] | | 0.56[b] | | | |
| | Herbaceous | −0.55[b] | 0.50[b] | −0.43[b] | 0.58[b] | | | |
| Support-limb diameter | Tree | | 0.23[b] | −0.22[b] | −0.24[b] | −0.22[b] | | |
| | Shrub | 0.57[b] | 0.68[b] | −0.13[c] | −0.21[b] | −0.16[c] | | |
| | Herbaceous | 0.62[b] | 0.49[b] | | | | | |
| Distance to trunk | Tree | 0.55[b] | 0.61[b] | | | −0.28[b] | | |
| Distance to periphery | Tree | 0.26[b] | 0.33[b] | −0.25[b] | | −0.21[b] | 0.60[b] | 0.30[b] |

[a] Nest height.
[b] Indicates $P < 0.01$.
[c] Indicates $P < 0.05$.

creased, cover below nests increased (Table 3). For tree nesters, cover both above and below the nest increased with greater relative nest height (Table 3), probably because relatively higher nests tended to be in the foliage zone of the canopy and thus were concealed better. The opposite relationship was found in herbaceous-nesting species; nests placed relatively higher in the nesting substrate had less cover (Table 3). Cover both above and below nests in trees and shrubs was negatively correlated with support-limb diameter. Generally, larger limbs had fewer small twigs and less foliage than did smaller limbs; thus, nests placed on larger limbs were less concealed.

The diameter of supporting limbs differed within the shrub- and tree-nesting assemblages (Table 2). The greatest variation in support-limb diameter occurred among the tree nesters, for which mean support diameter ranged from 0.7 cm for the Northern Oriole to 8.5 cm for the Blue

TABLE 4
CORRELATIONS OF NEST-SITE VARIABLES WITH THE FIRST TWO CANONICAL FUNCTIONS DERIVED FOR EACH SPECIES GROUP

| | Canonical function | | | | | |
|---|---|---|---|---|---|---|
| | Tree-nesting species | | Shrub-nesting species | | Herbaceous-nesting species | |
| Variable | I | II | I | II | I | II |
| Nest height | −0.56 | 0.74 | 0.90 | 0.09 | 0.85 | 0.49 |
| Support-structure height | −0.36 | 0.86 | 0.81 | −0.05 | 0.03 | 0.68 |
| Relative nest height | −0.37 | −0.23 | 0.21 | 0.18 | 0.97 | −0.01 |
| Cover above nest | −0.31 | −0.14 | −0.53 | 0.37 | −0.61 | 0.34 |
| Cover below nest | −0.11 | −0.26 | −0.43 | 0.79 | −0.53 | 0.04 |
| Support-limb diameter | 0.76 | 0.56 | 0.73 | 0.32 | | |
| Distance to trunk | −0.32 | 0.38 | | | | |
| Distance to periphery | 0.54 | 0.49 | | | | |
| Cumulative variance accounted for | 68.5 | 87.6 | 84.5 | 97.5 | 92.2 | 100.0 |
| Significance of canonical function[a] | <0.001 | <0.001 | <0.001 | <0.01 | <0.001 | 0.19 |

[a] Based upon minimizing Wilk's lambda.

Jay (Table 1). The Indigo Bunting had a smaller support-limb diameter than did other shrub-nesting species.

The distance of the nest from the trunk and periphery of the support differed among species nesting in trees (Table 2). These two measures were positively correlated with each other and with nest and support-structure height (Table 3). This suggests that species responded to variation in substrate width and were consistent in positioning the nest relative to the distance between tree trunk and periphery. Cover below the nest was negatively correlated (Table 3) with the latter two, suggesting that nests nearer the trunk or periphery were better concealed.

*Multivariate analyses.*—The first two canonical functions derived for tree-nesting species accounted for 88% of the variance in the data (Table 4). On the basis of correlations of these functions with the original variables, we interpreted the first function to represent a gradient of decreasing nest height and increasing support-limb diameter and distance to support periphery (Fig. 2). The second function was defined as a gradient of increasing nest and support-structure height. The Northern Oriole was well-separated from the other species on the first axis; this species had the greatest nest height and smallest support-limb diameter and distance to periphery (Table 1). The Eastern Wood-Pewee and Rose-breasted Grosbeak occupied an intermediate position on the first axis, and Blue Jays, American Robins, and Mourning Doves were located where the function

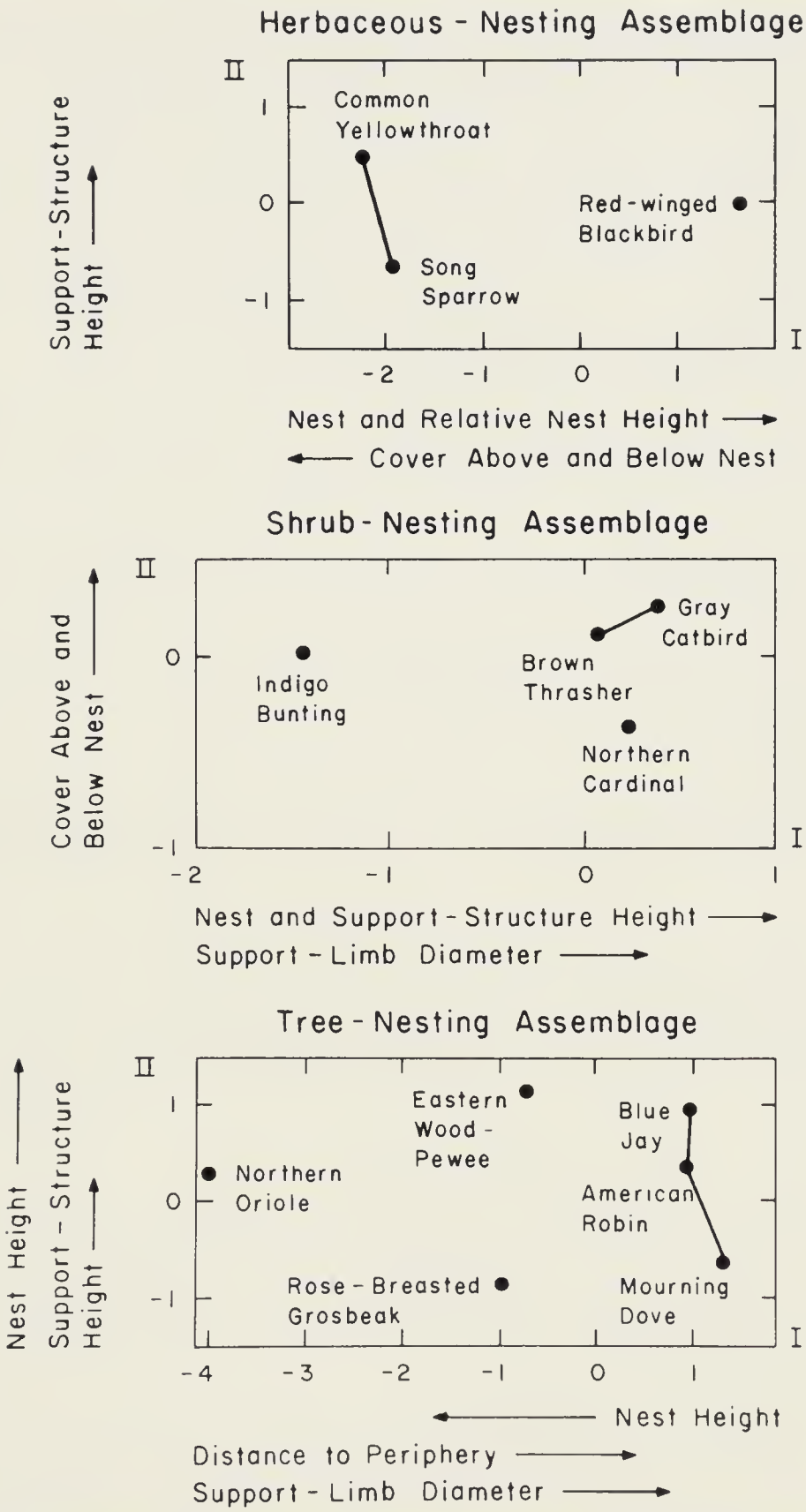


FIG. 2. Distribution of mean canonical scores along the first two canonical axes (I and II) of species nesting predominantly in trees, shrubs, and herbaceous cover. Species' means connected by a line do not differ ($P > 0.05$) in canonical space, as determined by Mahalanobis' distance.

represented the lowest nest height and the greatest distance to periphery and support-limb diameter (Fig. 2). The second axis separated the Eastern Wood-Pewee from the Rose-breasted Grosbeak and the Blue Jay from the Mourning Dove, primarily on the basis of support-structure and nest height. We conclude that all tree nesters we considered, except the American Robin, have nest sites distinctive from one another. On the basis of the variables used in the analysis, nest sites of American Robins did not differ significantly from those of Blue Jays and Mourning Doves, as determined by the significance of Mahalanobis' distance (Fig. 2).

From analysis of five nest-site characteristics, MacKenzie et al. (1982) also found that Northern Oriole nest sites were distinct from those of the other species. In contrast with our results, however, they reported significant differences between nest sites of Mourning Doves and American Robins. Although, in our study, nest sites of American Robins were similar to those of Mourning Doves and Blue Jays, their habitat-use patterns differed (Stauffer and Best 1980). Robins were most common in the savannah habitat, with wooded edge and floodplain woodland habitats also being used frequently. Blue Jays and Mourning Doves were most commonly encountered in upland woodlands; floodplain woodlands received the second most intensive use. Thus, even though some nest-site characteristics were similar, these species had different habitat-use patterns.

The first canonical function derived for the shrub-nesting assemblage was interpreted as a gradient of increasing nest and support-structure height and support-limb diameter (Fig. 2). On the first canonical axis, only the Indigo Bunting was distinct from the other species. The second canonical function, representing a gradient of cover above and below the nest, distinguished the Northern Cardinal from the Brown Thrasher and Gray Catbird, the latter two species having nest sites with greater cover (Fig. 2). These two functions represented 98% of the information contained in the original data (Table 4). Nest sites of Gray Catbirds and Brown Thrashers were not different in canonical space (Fig. 2), but habitat-use patterns differed between the two species. The upland woodland and scrub habitats were used most frequently by Brown Thrashers, whereas floodplain woodland and scrub habitats had the greatest use by Gray Catbirds (Stauffer and Best 1980). Thus, the potential for competition for nest sites between these two species may have been alleviated somewhat by their differential use of habitat.

Only the first canonical function was significant for herbaceous-nesting species (Table 4). This function represented a gradient of increasing nest and relative nest height and decreasing cover at the nest (Fig. 2). The Red-winged Blackbird was well separated from the other two species along this axis, tending to nest higher and at locations with less cover. The

second axis represented a gradient of increasing support-structure height and did not provide additional significant separation of the species (Fig. 2). On the basis of the nest-site variables that we used, nest sites of Song Sparrows and Common Yellowthroats were not different. Both Common Yellowthroats and Song Sparrows used wooded edge habitat most commonly, but yellowthroats also showed substantial use of floodplain woodlands, whereas Song Sparrows also frequently used herbaceous and scrub habitats (Stauffer and Best 1980).

Our results confirmed that, in many instances, substantial differences exist among the nest sites used by open-nesting (and cavity-nesting, see Stauffer and Best 1982) bird species breeding in riparian habitats. Most multivariate studies of avian community structure and composition have relied heavily on describing bird distributions along resource axes. These gradients usually are defined either by habitat characteristics recorded at locations where the birds were observed (e.g., James 1971, Anderson and Shugart 1974, Whitmore 1975, Smith 1977) or by foraging behavior (e.g., Rabenold 1978, Landres and MacMahon 1983, Sabo and Holmes 1983). Nest-site use is an important component of habitat selection in birds (Hildén 1965); presumably, habitats lacking suitable potential nesting substrates for a particular species will not be used as breeding sites by that species. Thus, when assessing species' interrelationships within a community, nest-site use should be considered (Collins 1981, Titus and Mosher 1981, Clark et al. 1983).

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# ASPECTS OF THE BIOLOGY OF THE HORNED SCREAMER IN SOUTHWESTERN COLOMBIA

LUIS G. NARANJO[1]

ABSTRACT.—An isolated population of the Horned Screamer (*Anhima cornuta*) in the Cauca Valley, Colombia, was studied intensively during 1983–1984. Variation of head plumage allowed me to identify individuals. This group of approximately 25 adults is the only breeding population of the species in southwestern Colombia. Home ranges were fairly large areas on the shoreline of the lagoon ($\bar{x}$ = 10.7 ha). Defense of home ranges involved both vocal displays and physical fights. Most activity occurred from 10:00 to 18:00. Long sessions of preening occurred during the early morning. Screamers fed on nine species of aquatic plants and were observed digging into mud. Besides preening and standing, seven comfort movements were identified: wing-shake, head-shake, tail-wag, wing-and-leg-stretch, two-wing stretch, one-wing stretch, and jaw-stretch. Of these movements, only the head-shake was performed as a part of the courtship behavior. Reproduction took place from late November to early May. Courtship involved social preening and an elaborate display performed by the male. Nests were floating platforms located within emergent vegetation. The average clutch size was 4.5 eggs, which were incubated by both sexes throughout the 47-day incubation period. *Received 17 June 1985, accepted 14 Oct. 1985.*

Information on the general behavior and ecology of the screamers (Anseriformes: Anhimidae) is meager. Recent literature on this group of waterfowl is based mainly on general field notes (Hudson 1920, Wetmore 1926, Weller 1967), and on observations in captivity (Stonor 1939, Lint 1956, Kupelberg 1959, Spence 1959, Bell et al. 1970). Only one paper is based on detailed field observations (Gill et al. 1974).

Two of the three species belonging to this family are distributed widely in Colombia. The Northern Screamer (*Chauna chavaria*) occurs in most of the Caribbean lowlands and the Horned Screamer (*Anhima cornuta*) occurs in the Amazonian region, the Eastern Llanos, and in two isolated populations in the Zulia and the upper Cauca valleys (Meyer de Schauensee 1949). No detailed field observations of these birds have been reported, except those by Gill et al. (1974). Other literature referring to screamers in Colombia includes only geographical notes, general observations, and descriptions of folklore (Olivares 1961, 1973; Rodriguez 1983).

During the last decade, personnel of the "Corporación Autónoma Regional del Cauca" (CVC), the government agency in charge of the management and conservation of wildlife in the Cauca Valley, have noted a decrease of the isolated population of the Horned Screamer in the region (O. Kaffury, pers. comm.). In order to evaluate the current status of this

[1] Dept. Biology, New Mexico State Univ., Box 3AF, Las Cruces, New Mexico 88003 and Dept. Biología, Univ. del Valle, A. A. 2188, Cali, Colombia.

population and to initiate a long term study of the species in Colombia, I made field observations on the general behavior, feeding ecology, population structure, and reproduction of this species in the Cauca Valley in 1983–1984.

## STUDY AREA AND METHODS

In the Cauca Valley, the Horned Screamer occurs in only two localities near Buga: the "Laguna del Choncial," a highly disturbed area where only four screamers have been observed during monthly visits in the last three years (O. Kaffury, pers. comm.), and the Natural Reserve "Laguna de Sonso" where the species has been reported breeding.

Most of my observations were made at the latter locality. The Laguna de Sonso is a large, approximately 594-ha marsh located near the eastern bank of the Cauca River (03°52′N, 76°21′W, 935 m above sea level) (Fig. 1).

Because of periodic flooding, the depth of the lagoon and its area fluctuate greatly. Most of the lagoon is covered with water hyacinth (*Eichornia crassipes*) and, to a lesser extent, water lettuce (*Pistia striatiotes*). The shoreline supports a wide belt of emergent vegetation with scattered trees and shrubs (mainly *Salix humboldtiana, Erythrina fusca, Laetia acuminata,* and *Fagara pterota*). The area is permanently protected from hunting and use of motor boats, but there is some fishing by local inhabitants, and the surrounding area is used intensively for grazing cattle and for cultivation.

The study included weekly observations from April 1983 through May 1984 (1–3 days per week; total observation time per week was 8–24 h). Most attention was given to activity patterns, but I also noted population size, home range size, and group composition. Birds were observed with 8 × 30 binoculars and a 60× spotting scope from a 6-m tower on the western border, and from portable blinds within the home ranges of the screamers. Observations were tape-recorded, and the time of each behavioral bout measured. Most of the behavioral patterns were also photographed using a camera with 400-mm telephoto lens and motordrive.

Because of the unpredictability of the water level in the area and the difficulty of detecting some of the birds while they were active on the ground, timing of the observations was opportunistic, and an accurate description of seasonal variation of behavior is not possible. Activity was recorded, however, during almost every hour of the day, and some generalizations of the daily timing of each pattern are thus included. Population size was estimated using two different methods. First, because Horned Screamers are sedentary (Gill et al. 1974), the locations of birds inhabiting the western shore of the lagoon, where most of the observations were made, were mapped whenever they were observed. This was facilitated by recognition of distinctive patterns of head plumage of individuals (Fig. 2). This method also allowed me to determine the boundaries of the seven home ranges studied. Second, the screamers on the eastern border of the lagoon were counted repeatedly from the tower during early morning, when the birds were perched on the tops of shrubs and trees.

Voucher photographs of the study area and of Horned Screamer's home ranges, nests, eggs, and chicks, have been deposited in VIREO (Visual Resources for Ornithology, Academy of Natural Sciences of Philadelphia, 19th and The Parkway, Philadelphia, PA 19103) under catalog numbers N02-1-001 through N02-1-007.

## ABUNDANCE AND POPULATION STRUCTURE

The combined survey methods yielded an approximate, but conservative, estimate of 25 adult birds (censuses averaged 24.6 ± 1.9 individuals [SD], N = 11).

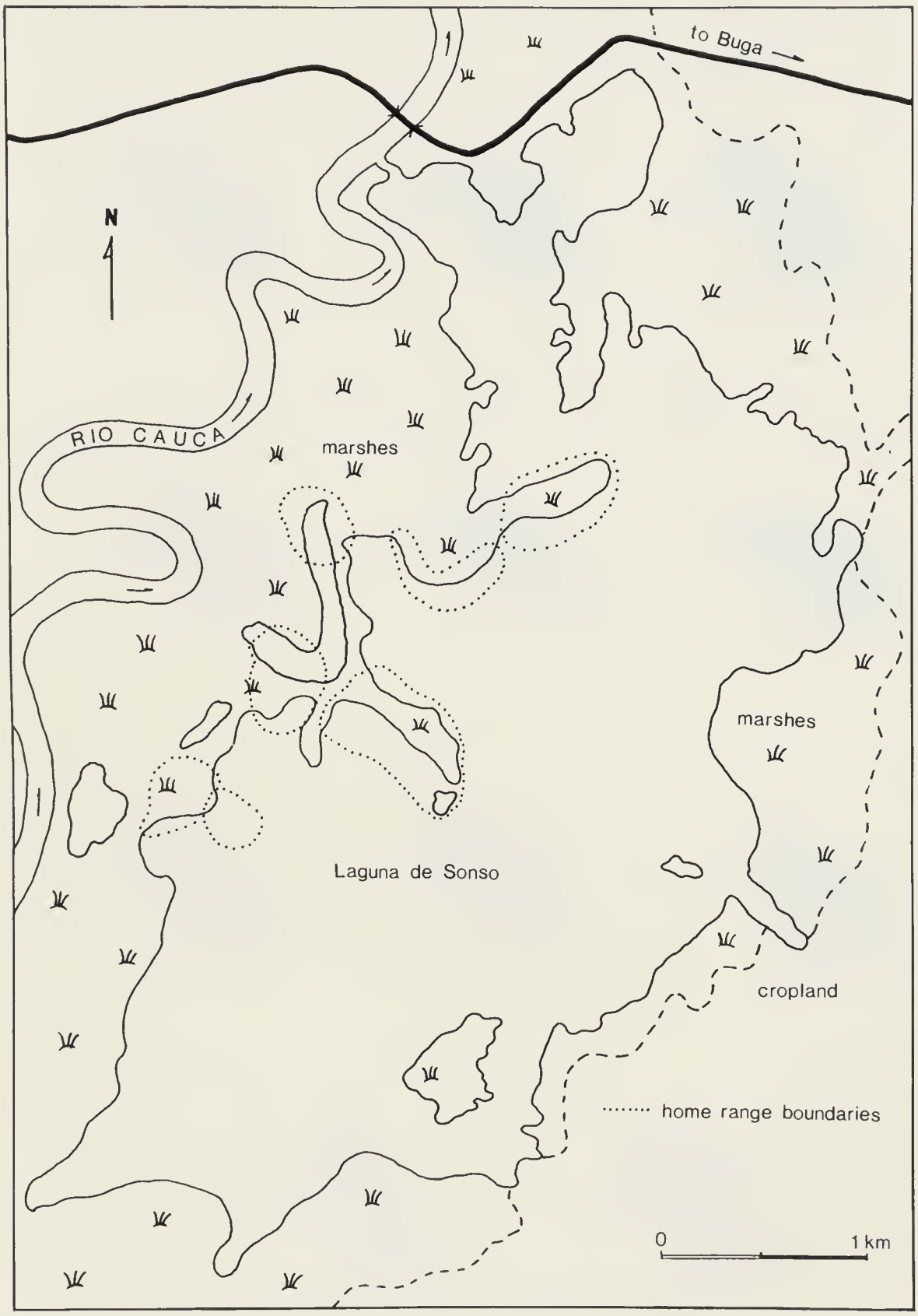


FIG. 1. Laguna de Sonso and adjacent marshes, showing the locations of the seven home ranges.

FIG. 2. Variation in the head plumage of the Horned Screamer in Sonso. Drawings were made on the site and are based on close range observations.

With one exception, pairs of adults observed were stable throughout the year. The exceptional case was a pair observed sporadically from September to November 1983; by March 1984 the female of this pair was replaced by another bird that had been seen alone earlier in a neighboring area. Of the seven home ranges studied, two were occupied by family groups, composed of three and four individuals, respectively. I observed the group of four individuals carefully during 10 months, beginning in March 1983. Two of the birds lacked the characteristic horn-like feather on the forehead, and were probably yearlings; they habitually followed the other two individuals closely. In November 1983, one of the apparently young birds, at that time exhibiting a short horn, started to court the adult female. This bird was repelled repeatedly by the adult male. One month later, when the adults were observed performing courtship and copulation behavior, the two young individuals had disappeared from the area.

The other group was composed of three individuals in adult plumage; changes of the structure of this group were not detected. These observations seem to be in accordance with the strong pair bonds suggested by Todd (1979) for screamers, and the low gregariousness reported for the species by Gill et al. (1974).

## HOME RANGE

Each of the seven studied ranges included a large area on the shoreline ($\bar{x} = 10.7 \pm 8$ ha) (Fig. 1); aquatic boundaries varied according to the amount of floating vegetation moved around by the wind.

Most of the area occupied by the screamers was flooded permanently, and birds waded within the emergent vegetation or walked on the floating masses of water hyacinth while feeding; but I never observed birds swimming. Birds used emergent ground only when it was covered with aquatic food plants. Six of seven home ranges included at least one tree (*Salix humboldtiana, Erythrina fusca, Laetia acuminata*) or some shrubs (mainly *Fagara pterota*) that were used as perches. In the only area that lacked a perch, the two birds using it started to perch on a blind within their boundaries, immediately after its construction.

Although direct evidence of territoriality is scarce, some data suggest that the home ranges of the screamers might actually be defended territories. Each day screamers performed one or more choruses of loud calls. Most of the vocalizations were produced while the birds were perched; birds were more silent when searching for food on the ground. The screams initiated by one adult or a group of birds often resulted in vocalizations by neighbors (such a response was detected in 76% of the choruses observed by Gill et al. 1974 and in 100% of those in the present study).

I saw birds defend territories twice in the Laguna de Sonso. On 14 October 1983, a group of four individuals was searching for food at 09:44 when a bird flew above them and landed nearby. The four birds took off immediately, landed within 2 m of the bird, and pursued it for 19 sec. The group kept their necks inflated and partially retracted, the bills close to the neck feathers, the dorsal plumage erected, and their shoulders pointing forward with the spurs conspicuously exhibited while they rapidly flapped their wings. The intruder flew out of the area, and the four birds then performed a vocal chorus, shaking their heads and necks, for 58 sec.

On 30 December 1983, a pair of screamers not previously seen in the area arrived within the border of the home range of the same family group cited above, and perched on a tree for about 4 h. At 10:11 the pair flew toward the middle of the home range and landed about 30 m from the resident female, which immediately flew to a point less than 5 m from the intruders, inflated her crop, erected her dorsal plumage while pointing her spurs forward, and initiated a series of loud vocalizations that were answered by one of the intruders (the other flew out of the home range after the female approached). The vocalization period lasted 4 min, during which time the foreign bird called seven times ($\bar{x}$ = 7.7 sec), and its opponent called three times ($\bar{x}$ = 6.6 sec). The intruder then left the area, followed by the resident female 2 sec later. Upon reaching the border of the home range, the female landed and remained in an alarm posture for 7 min, before returning to the center of the home range.

The fact that only two territorial displays were observed may be a reflection of the reduced size of the population in the area. Weller (1967) and Todd (1979) noted that screamers become involved not only in aggressive displays, but also in actual fights; and both authors mentioned broken spurs found in the breasts of some of their birds.

## FEEDING BEHAVIOR AND DIET

With only a few exceptions, screamers fed from mid-morning (10:00) until late afternoon (18:00). Birds alternated the search for food with periods of standing, preening, and walking or flying. Two components of feeding behavior were observed.

The most frequent feeding behavior (97.2% of the total feeding time) was grazing. As previous workers (Weller 1967, Todd 1979) reported, the screamers are mainly if not completely herbivorous. In Sonso, the Horned Screamers fed on at least nine different plants, which they took while walking or wading slowly across their home range. Screamers grazed by pecking at leaves, vines, stems, and flowers with lateral movements of

the head, and swallowed the food items immediately, except when the food was longer than their bills, as in the case of water hyacinth inflorescences (Fig. 3A–C). Plants included in screamer diets and the proportion of occurrence of each (percentage of the observed grazing time) were as follows: *Hydrangea,* 56.4%; *Eichornia crassipes,* 14.9%; *Polygonum hispidum,* 5.6%; *Paspalum dilatatum,* 5.1%; *Artemisia absinthium,* 3.1%; *Aeschynomene ciliata,* 1.4%; *Pistia striatiotes,* 1%, *Cardiospermum carendum,* 0.4%; and unidentified plants, 12.1%.

The second most common feeding behavior (2.6% of the total feeding time) was digging. Although I am not certain that the screamers actually took food while digging, they were observed making swallowing motions after each digging bout. Birds waded slowly in shallow free water, and moved their bills into the mud with rapid backward strokes of the head. The behavior resembles the digging behavior of the Magpie Goose (*Anseranas semipalmata*) (Davies 1963), although I do not know if the screamers "filtered" while they dug. Olson and Feduccia (1980) reported the presence of vestigial lamellae both in the upper and lower mandibles of the Horned Screamer, which suggests the possibility of occasional filtering.

I observed screamers drinking briefly on two occasions. Perhaps the succulence of the plants used by these birds as food accounts for the infrequent occurrence of this behavior. A bird drank while wading in shallow water; it dipped its bill into the water and lifted its head, swallowing the drink immediately.

## COMFORT BEHAVIOR

The behavioral patterns here described are based upon 73 detailed observations of nearly 15 min each of 14 different adults. The general behavior of the screamers was classified into five categories, comprising movements with variable frequency and proportion of occurrence. The names given to each of these movements follow McKinney's nomenclature (1965), with the exception of standing and sleeping, which were not described by him. Although the total number of samples was low and the proportion of samples per hour varied, some generalizations can be made by grouping the observations into 4-h periods to show the general activity sequence during the day (Table 1). Because of their high percentage of occurrence in the activity of the screamers, both standing and preening are included in the table as separate entries. The behavioral categories and their component movements are described as follows:

*Standing.*—Screamers alternate every activity with periods of standing. Although only a slight variation in the proportion of the time spent stand-

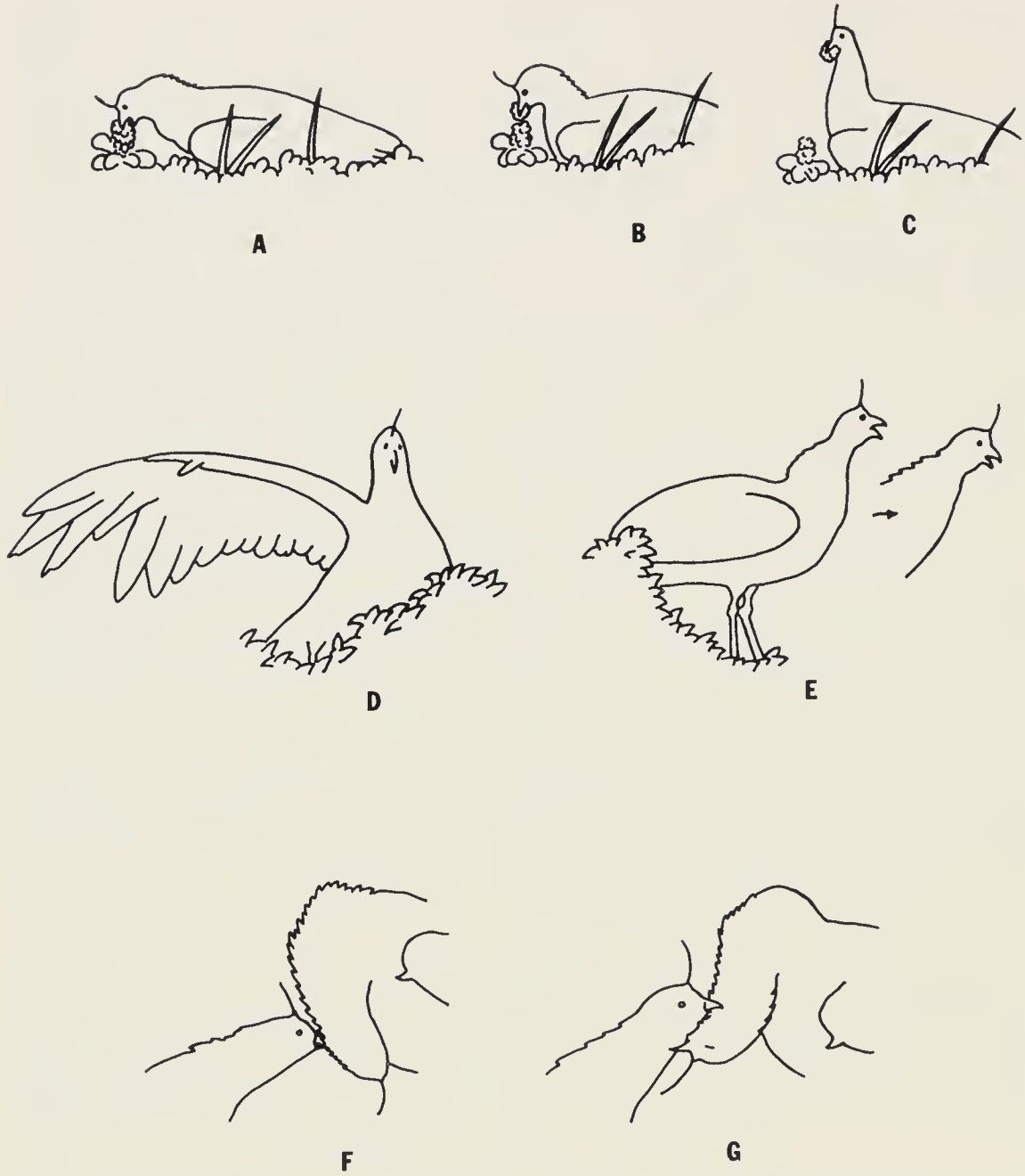


FIG. 3. Behavioral movements of the Horned Screamer: (A–C) Grazing, (D) One-wing stretch, (E) Calling, (F–G) Social-preening. All drawings were made from 35 mm photographs of individuals in the field.

ing was observed, standing occupied a higher proportion of the time as the day progressed (Table 1). Screamers stood with their necks partially retracted, wings folded, and, for brief periods, one foot raised.

*Preening.*—Most preening occurred during the early morning while the screamers were perched on trees and shrubs; time spent preening decreased progressively through the rest of the day (Table 1). Preening included almost every part of the body, with most time spent on breasts,

TABLE 1

MEAN DURATION ± SD PER SEQUENCE AND PERCENTAGE OF TOTAL TIME SPENT IN DIFFERENT BEHAVIORAL PATTERNS

| Behavior | Morning[a] | | | Midday | | | Evening | | |
|---|---|---|---|---|---|---|---|---|---|
| | N[b] | $\bar{x}$[c] ± SD | % | N | $\bar{x}$ ± SD | % | N | $\bar{x}$ ± SD | % |
| Preening | 150 | 13.0 ± 5.6 | 27.9 | 288 | 6.7 ± 3.2 | 10.9 | 148 | 7.0 ± 2.8 | 5.9 |
| Comfort | 14 | 5.7 ± 1.8 | 1.2 | 44 | 4.0 ± 1.2 | 0.6 | 18 | 3.5 ± 0.4 | 0.2 |
| Locomotion | 3 | 6.7 ± 0.0 | 0.2 | 36 | 12.9 ± 5.8 | 2.4 | 24 | 17.0 ± 4.4 | 2.0 |
| Feeding | 24 | 36.9 ± 40.2 | 9.0 | 247 | 15.0 ± 9.9 | 17.0 | 266 | 11.4 ± 4.0 | 20.4 |
| Calling | 7 | 2.9 ± 0.5 | 0.2 | 22 | 7.6 ± 2.4 | 0.6 | 7 | 5.4 ± 0.0 | 0.2 |
| Social[d] | 14 | 12.5 ± 5.0 | 1.8 | 13 | 11.2 ± 12.4 | 0.5 | 12 | 5.4 ± 3.2 | 0.2 |
| Agonistic | 1 | 21.0 ± 0.0 | 0.2 | 3 | 6.0 ± 0.7 | 0.1 | 0 | | 0.0 |
| Sleeping | 0 | | 0.0 | 4 | 91.3 ± 4.7 | 1.0 | 0 | | 0.0 |
| Standing | 195 | 34.2 ± 40.1 | 59.5 | 599 | 56.7 ± 70.5 | 66.9 | 477 | 56.5 ± 53.7 | 71.1 |

[a] Morning = 06:30–10:30 (total time of observation 8911 sec), Midday = 10:30–14:30 (29,701 sec), Evening = 14:30–18:30 (22,548 sec).
[b] N = number of sequences observed.
[c] $\bar{x}$ and SD in seconds.
[d] Social = Social-preening and Head-bobbing.

wings, and sides. Only a small proportion of preening involved scratching the head. Birds grasped feathers with their bills while preening, and preening perches were easily recognized by the numerous feathers, including remiges, on the ground (screamers undergo a graduated wing molt [Haffer 1968, Todd 1979]).

The following three shaking movements were associated mainly with preening and standing.

*Wing-shake.*—The bird slightly raised one wing, then the other, and then folded them, usually after preening the sides or the wing coverts ($\bar{x}$ = 3.6 ± 0.7 sec [SD], N = 5).

*Head-shake.*—After preening or feeding bouts, the birds sometimes shook the head from side to side for 3.9 ± 1.01 sec (N = 7). A secondary situation in which this movement occurred (Head-flick) will be discussed under courtship behavior.

*Tail-wag.*—The bird depressed its tail and moved it rapidly from side to side 1–4 times while standing. Two bouts of 3.5 sec each were observed.

The following three stretching movements were only observed after long sessions of preening and standing:

*Jaw-stretch.*—The bird stretched its neck and widely opened its beak, which was pointed upward ($\bar{x}$ = 2.8 ± 0.2 sec, N = 11).

*Wing-and-leg stretch.*—The bird fully stretched one wing laterally, or both the wing and leg of the same side directed backward ($\bar{x}$ = 6.5 ± 3 sec, $N$ = 7). The one-wing-stretch movement (Fig. 3D) is not mentioned for the Anatidae by McKinney (1965).

*Both-wings stretch.*—The bird slowly flapped the partially or fully extended wings, with the neck fully erected or inclined forward ($\bar{x}$ = 5.25 ± 0.7 sec, N = 10).

*Sleeping.*—I observed screamers sleeping four times. All of the observations were in the middle of the day, when the birds were on their feeding grounds. The birds rested with their eyes closed and their bills on their retracted necks or buried within their back feathers.

## LOCOMOTION

The proportion of daily activity dedicated exclusively to locomotion was very small; most movements were from one foraging site to another. More time was spent moving in midday than during early morning or late afternoon (Table 1). The average duration of flying bouts was 5 ± 0 sec (N = 8), and that of walking and wading was 22.2 ± 20.0 sec (N = 23). Screamers flapped their wings a few times and then soared until landing. Hudson (1920) observed frequent soaring by the Southern Screamer (*C. torquata*), but in Sonso the screamers were not observed soaring.

## VOCALIZATIONS AND SOCIAL BEHAVIOR

Gill et al. (1974) described in detail the vocalizations of this species. At Sonso, I noticed no daily variation in the proportion of time spent calling, but the average duration of the calling bouts (Table 2) appeared to be longer during the midday. While calling, the screamers stretched their fully inflated necks, and shook their heads (Fig. 3E).

*Head-bobbing.*—When one screamer approached its partner on the ground or landed on a perch beside it, both birds shook their heads upwards 1–3 times while keeping their necks stretched ($\bar{x}$ = 2.35 ± 2.2 sec, N = 14).

*Social-preening.*—Often when the two members of a pair were standing together, they preened the feathers of each other's heads and necks ($\bar{x}$ = 21.1 ± 30.4 sec, N = 7) (Fig. 3F–G). Stonor (1939) mentioned this display as the main courtship behavior; in the present study the birds performed it throughout the year.

## AGONISTIC BEHAVIOR

Agonistic behavior was observed only when the screamers were attacked by flying Southern Lapwings (*Vanellus chilensis*). When a flying lapwing approached a standing screamer, the latter stretched its neck in the alarm posture and then bowed, keeping the neck pointing forward. After the attack, the screamer called loudly (1–4 times, $\bar{x}$ = 9.8 ± 7.5 sec, N = 4).

## REPRODUCTION

*Courtship behavior.*—Stonor (1939) noted that apart from allopreening displays, the Southern Screamer does not exhibit any definite courtship behavior. Horned Screamers, however, in addition to the frequent mutual preening observed throughout the study, sometimes performed a display immediately before copulation. In this display, which I saw on four occasions, the male walked around the standing female with his bill pointing downward against his inflated crop, his neck retracted, his dorsal feathers partially erected, and his wings partially opened with the carpal joint pointing downward. After circling, the male bowed 1–3 times in front of the female ($\bar{x}$ = 84.5 ± 92.3 sec, N = 4). In one case preceding this display, the male shook his head in a circular motion during 3 sec, flew in a wide circle for 30 sec, returned to his departure site in front of the female, and then began to court her. The circular motion of the head by the male corresponds to the Head-flick described by McKinney (1965), and found as a precopulatory movement within the Anatidae only in the Red-crested Pochard (*Netta rufina*).

*Aggression.*—As mentioned before, pairs were stable throughout the

year, and apparently juveniles remained with their parents during their first year of life. In one case, a juvenile courted an adult female repeatedly, and was chased with increasing frequency by the adult male. Most chases were simple running pursuits in which the adult male inflated his crop and directed his spurs forward. In one case, the two birds grasped each other's necks with their bills, and shook their wings rapidly with their spurs directed toward each other. The fight lasted 40 sec, after which the adult male abandoned the site, and both the female and the juvenile vocalized in duet eight times during 12 sec.

*Copulation.*—I saw two copulations, both by the same pair (6 November 1983 at 07:10, 2 December 1983 at 11:49 during a feeding session). Without any preliminary display, the male mounted the female for 10 sec, while grasping her horizontally extended neck with his bill, and flapped both wings slowly during copulation.

*Nests and eggs.*—Because of the dense vegetation in the nesting areas and floods at the beginning of the nesting period, only two nests were detected. On 28 January 1984, one nest was discovered when it was carried out of the lagoon in a floating mass of vegetation. The nest was partially destroyed, and I collected the eggs and attempted (unsuccessfully) to hatch them in an incubator. The second nest was found on 1 April 1984. It was situated in a small pond adjacent to the lagoon, encircled by tall grasses, rushes, and bushes. The structure was a platform floating over 116 cm of water, formed of water hyacinth plants covered with dry *Paspalum dilatatum*. It was 65 cm in diameter, 12 cm above the water level, with a shallow depression in the middle that contained the eggs.

The eggs were oval, with the ground color varying from almost pure white to buffish, mottled with cinnamon brown. Eggs measured 84.6 × 61.02 ± 3.2 × 1.9 mm, and weighed 149.9 ± 11.02 g (N = 9).

*Incubation.*—Incubation by both sexes was reported by Stonor (1939) for the Southern Screamer, and by Lint (1956) for a pair of captive Horned Screamers. Because the nest was not directly detectable from the observation site in Sonso, shifts in incubation were inferred from the observed arrival and departure of birds at the nest site. I distinguished the sexes by individual differences in the head plumage of copulating birds. The female remained at the nest during most of the daylight hours and was replaced by the male for short periods. The male was at the nest for most of the night. Diurnal sessions averaged 65.6 ± 61.2 min (N = 7) for the male, and 194.2 ± 106.5 min (N = 6) for the female. Nocturnal sessions averaged 830 ± 83.1 min (N = 3) for the male and 934 min (N = 1) for the female.

When the nest was discovered (1 April 1984), it contained three eggs.

When I checked the nest seven days later, it contained an additional egg. As Stonor (1939) noted that the Southern Screamer does not begin to incubate until the clutch is complete, the incubation period for this nest was between 40 and 47 days; this agrees with the 44-day artificial incubation period reported for a captive Horned Screamer clutch by Lint (1956).

## EVOLUTIONARY RELATIONSHIPS

Researchers disagree on whether the resemblances of behavioral patterns of the Magpie Goose and the Anhimidae are due to a close phylogenetic relationship or to convergence (Johnsgard 1961, Davies and Frith 1964); recent information from biochemical and anatomic studies (Brush 1976, Olson and Feduccia 1980) support the former interpretation. Digging as a component of the feeding behavior of the Horned Screamer, and social preening observed both in this study and for the Southern Screamer (Stonor 1939) support this proposed relationship. Other behavioral patterns described in the present paper do not provide conclusive evidence to favor either hypothesis. Further study aimed at identifying secondary displays derived from the comfort movements would help clarify this problem.

## CONSERVATION

The results of the censuses of the present study showed that the population size of the species in the region is extremely small (25 adult birds). There is no evidence of decrease for the last five years, taking into account estimations made by personnel of the CVC. At both of the localities where the species is found west of the Eastern Andes, habitat appropriate for screamers is shrinking because of sedimentation and plant succession, accelerated by drainage of marshes and cultivation on the surrounding areas. I believe that unless some programs of habitat preservation are initiated, sufficient suitable habitat for the species will decline, and extirpation of this isolated population is likely during the next few years.

## ACKNOWLEDGMENTS

I want to dedicate this paper to my wife Carmen Cecilia, whose company in the field and continuous encouragement made it possible to surmount the most difficult parts of the field work. My field assistant, W. Beltrán, merits special acknowledgment because his efforts and valuable suggestions during the field work were more than helpful. Finally, I want to thank I. Cabrera for the taxonomic identification of plants, and R. J. Raitt for his suggestions and advice during the preparation of the manuscript, and H. Alvarez for setting me on the track of the screamers. This research was possible thanks to the financial support from Colciencias (Grant 10006-1-35-83) and the Universidad del Valle (Grant 911-056-12-82).

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# SOME ASPECTS OF THE BREEDING BIOLOGY OF RED-WINGED BLACKBIRDS IN ALASKA

A. David McGuire[1]

Abstract.—Red-winged Blackbirds (*Agelaius phoeniceus*) reach the northern limits of their breeding range in eastern interior Alaska. Blackbird breeding phenology in Alaska is more synchronous, eggs are larger, nestlings grow more rapidly, and clutch-size and female reproductive success are higher than in populations farther south. The lack of a difference in the rate of tarsometatarsus increase in conjunction with the faster growth rate of nestlings suggests that the differences I found between this and more southerly populations are environmental responses to abundant food resources in the nestling period. *Received 16 Jan. 1984, accepted 21 Oct. 1985.*

The Red-winged Blackbird (*Agelaius phoeniceus*), one of the most intensively studied passerines in North America, has a polygynous mating system best termed resource-defense polygyny (Emlen and Oring 1977). From 0 to 12 females (Orians 1980) may nest on a territory defended by a male. During the breeding season redwings are usually associated with cattail (*Typha* spp.) or bulrush (*Scirpus* spp.) marshes (Orians 1980), but they can also be found in some upland habitats (Robertson 1972).

Red-winged Blackbirds breed from northern Costa Rica to the subarctic taiga forests of Canada and eastern interior Alaska (A.O.U. 1983). Studies of the Red-winged Blackbird in Alaska are important because aspects of the breeding biology of the species at the northern limits of its range may differ from those of populations farther south. This paper compares the breeding biology of a population of redwings in eastern interior Alaska to that of other populations farther south.

## STUDY AREA AND METHODS

The study was conducted near Northway, Alaska (62°58′N,141°56′W), a village in the Northway-Tanacross lowlands where the Chisana and Nabesna rivers converge to form the Tanana River. Redwings breed in this area around ponds and lakes in stands of cattail (*Typha latifolia*) and bulrush (*Scirpus validus*). I checked 43 lakes and ponds for redwing activity, but only the 7 listed in Table 1 had breeding blackbirds.

I studied the biology of redwings from 10 May to 7 July 1981 and from 11 May to 6 July 1982. I began intensive and systematic searches for nests on 1 June 1981 and on 6 June 1982, and continued each year until all male territories had been searched for nests. Weather permitting, I visited nest sites at 4-day intervals in 1981 and every 3 days in 1982. Length and breadth of eggs were measured to the nearest 0.25 mm using Bel Art dial Type 6932 calipers. Each egg was individually marked for later identification. Nestlings in the

[1] Dept. Biology, Fisheries, and Wildlife, Univ. Alaska, Fairbanks, Alaska 99701.

TABLE 1

LAKES AND NUMBERS OF BREEDING MALE AND FEMALE RED-WINGED BLACKBIRDS

| Lake | Approximate area (ha) | 1981 | | 1982 | |
|---|---|---|---|---|---|
| | | Males | Females | Males | Females |
| Hudeac Lake | 12.9 | 2 | 3 | 2 | 3 |
| Pond Southeast Hudeac Lake | 6.4 | 1 | 1 | 0 | 0 |
| Lake at west end Northway | 6.4 | 1 | 4 | 1 | 5 |
| Tractor Trail Lake | 12.9 | 1 | 3 | 1 | 1 |
| Andrew Lake | 25.7 | 3 | 6 | 4 | 8 |
| Julius Lake | 45.0 | 9 | 16 | 8 | 17 |
| Shashamund Lake | 36.7 | 7 | 12 | —[a] | — |

[a] Not studied in 1982.

nest were weighed at each visit with a Pesola spring balance. Length of the right tarsometatarsus of each nestling was measured to the nearest 0.25 mm.

Each nestling was individually marked with a black indelible ink pen on a combination of the left or right tibia and tarsometatarsus. Some females removed banded nestlings less than 6 days old from the nest, so nestlings were not banded until I judged that fledging was imminent (when young were 7–8 days old). Nestlings were assumed fledged if they were not present in the nest on or after 9 days of age and had appeared healthy on the previous visit to the nest.

Egg volume was calculated as 0.524 × length × breadth$^2$ (Preston 1968). The weight and length of tarsometatarsus on day one were considered as measurements taken within 24 h of hatching. I used the total number of first nesting attempts in order to calculate clutch-size per nest, number of eggs hatched per nest, and number of young fledged per nest. Nests from which females removed banded nestlings (9 nests in 1981) were not used in calculations of breeding success, fledging success, number of young fledged per nest, or brood-size dependent growth rates.

Tests of statistical difference were performed according to Zar (1974), Conover (1980), and Biomedical Computer Program (Dixon 1981) statistical software. Parametric statistics (e.g., two-sample *t*-tests) were employed if the data passed tests for normality. Otherwise, comparable nonparametric statistics (e.g., Mann-Whitney *U*-tests) were used in the analyses. Unless otherwise specified, each null hypothesis was rejected if the test statistic exceeded the value of $P > 0.05$.

## RESULTS

Two male Red-winged Blackbirds were present at the east end of Hudeac Lake on the afternoon of 10 May 1981 as ice was breaking up on the lake. I saw no female redwings during daily visits to ponds with cattails until 17 May 1981.

In 1982 observations at the breeding areas commenced on 11 May. The first male redwing was noted at Julius Lake late on 14 May when edges of the lake were ice-free. The first female appeared at Hudeac Lake

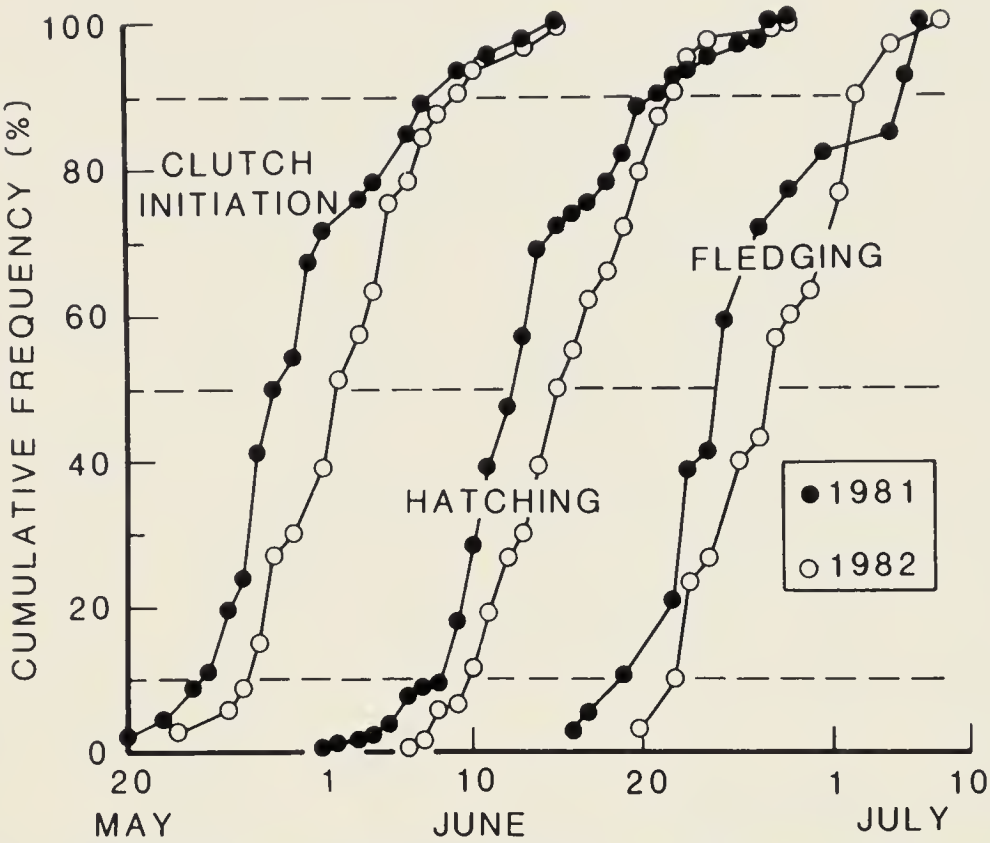


FIG. 1. Cumulative frequency of clutch initiation, hatching, and fledging phenology for 1981 and 1982.

on 22 May 1982, by which time the ice on the study lakes was breaking up.

In 1981 snow melted by 30 April, but in 1982 snow remained on the ground until 8 May (National Weather Service). Likewise, lakes which were melting on 10 May in 1981 did not achieve an equivalent stage of melt-off until around 20 May in 1982. Although ice breakup on the lakes differed by about 10 days, the breeding seasons seemed to be separated by only 3 days in the two years of this study (Fig. 1).

The phenological curves for 1981 and 1982 converge in the later half of each of the clutch initiation, hatching, and fledging sub-seasons (Fig. 1). The number of active nests peaked on 11 June in 1981 and 13 June in 1982 (Fig. 2); however, in both 1981 and 1982, 90% of the clutches were started by 9 June (Fig. 1).

Mean egg length was 25.0 mm in 1981 (N = 169) and 25.5 mm in 1982 (N = 138). Mean egg breadth was 18.0 mm in 1981 and 18.4 mm in 1982. Egg length, breadth, and volume were all significantly larger in 1982 (for length: $U = 9635$, df = 1, $P = 0.0087$; for breadth: $U = 8515$, df =

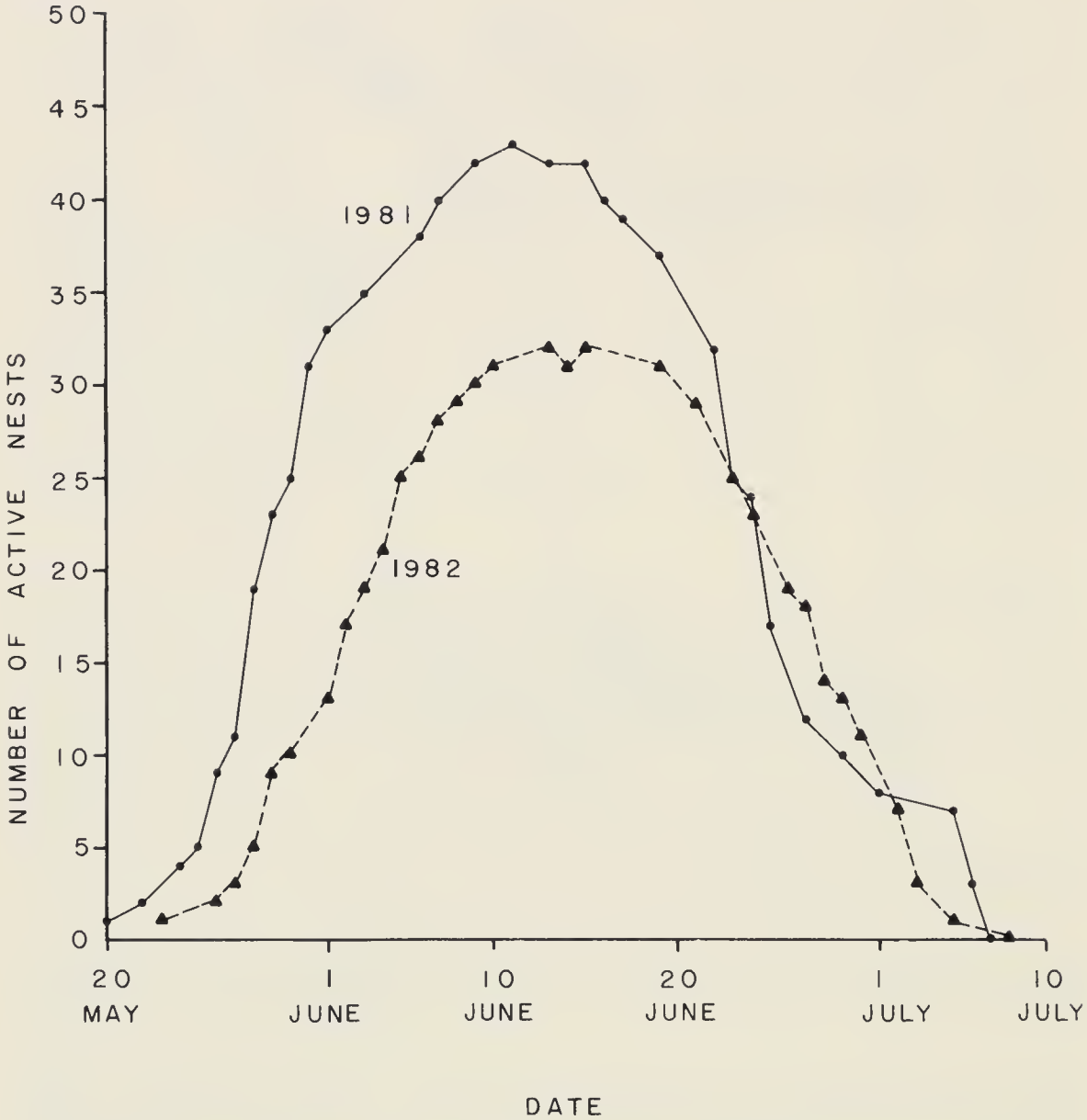


FIG. 2. Number of active nests as a function of date in the breeding season.

1, $P < 0.0001$; for volume: $U = 8488$, df = 1, $P < 0.0001$). Mean clutch-size was 4.4 eggs in 1981 (N = 37) and 4.3 eggs in 1982 (N = 34) ($U$ = 576, df = 1, $P$ = 0.4838). Modal clutch-size in both years was 4 eggs. Mean number of eggs hatched per nest was 3.9 in 1981 and 3.6 in 1982 ($U$ = 672, df = 1, $P$ = 0.6032). In 1981 and 1982, 11.1% and 15.5%, respectively, of the eggs laid did not hatch.

Mean number of nestlings fledged per nest was 3.4 in 1981 and 3.5 in 1982 ($U$ = 616, df = 1, $P$ = 0.8720). In 1981 and 1982 12.8% and 4.2%, respectively, of the eggs hatched did not fledge. Percent hatching success and breeding success (nestlings fledged/eggs laid) were equally high for different clutch-sizes (Table 2). Fledging success (nestlings fledged/eggs

TABLE 2

PERCENT HATCHING, FLEDGING, AND BREEDING SUCCESS BASED ON CLUTCH-SIZE AND NUMBER OF EGGS HATCHED PER NEST

| | Clutch size | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | Total |
| Hatching success | | | | | | | |
| 1981 | 0 (1)[a] | 0 (1) | 100 (2) | 90 (24) | 99 (16) | — | 92 (44) |
| 1982 | — | 100 (1) | 100 (2) | 84 (17) | 85 (12) | 100 (1) | 86 (33) |
| Total | 0 (1) | 50 (2) | 100 (4) | 97 (41) | 93 (28) | 100 (1) | 90 (77) |
| Breeding success | | | | | | | |
| 1981 | 0 (1) | 0 (1) | 100 (2) | 78 (23) | 93 (11) | — | 83 (38) |
| 1982 | — | 100 (1) | 50 (2) | 81 (17) | 82 (12) | 100 (1) | 81 (33) |
| Total | 0 (1) | 50 (2) | 75 (4) | 79 (40) | 87 (23) | 100 (1) | 82 (71) |
| | Number of eggs hatched per nest | | | | | | |
| | | 2 | 3 | 4 | 5 | 6 | Total |
| Fledging success | | | | | | | |
| 1981 | | 100 (1) | 83 (6) | 90 (18) | 94 (10) | — | 91 (35) |
| 1982 | | 100 (2) | 83 (10) | 100 (10) | 100 (8) | 100 (1) | 96 (31) |
| Total | | 100 (3) | 83 (16) | 94 (28) | 97 (18) | 100 (1) | 93 (66) |

[a] % (number of nests).

hatched) also was equally high across different initial brood sizes. Ninety-three percent of the chicks that hatched fledged, and more young fledged from nests of the nonmodal clutch-size of five than from the modal clutch-size of four.

Average nestling weight at day seven was independent of number of young fledged per nest (Fig. 3). Thus large and small broods fledged young of similar weight. Weight did not appear to be at an asymptote at the time of fledging (Fig. 4).

## DISCUSSION

The adaptive significance of life history parameters such as clutch-size and development rates has been the focus of much attention in recent years. Most of the literature on life history parameters has concerned comparisons across species (e.g., Lack 1968; Ricklefs 1968, 1973). However, understanding the variability of these parameters within a species is essential to understanding their adaptive basis.

Except possibly for redwings breeding in Minnesota (Moulton 1981), in which the median clutch initiation date and the date of first clutch initiation were separated by only 7 days, the synchrony observed for the

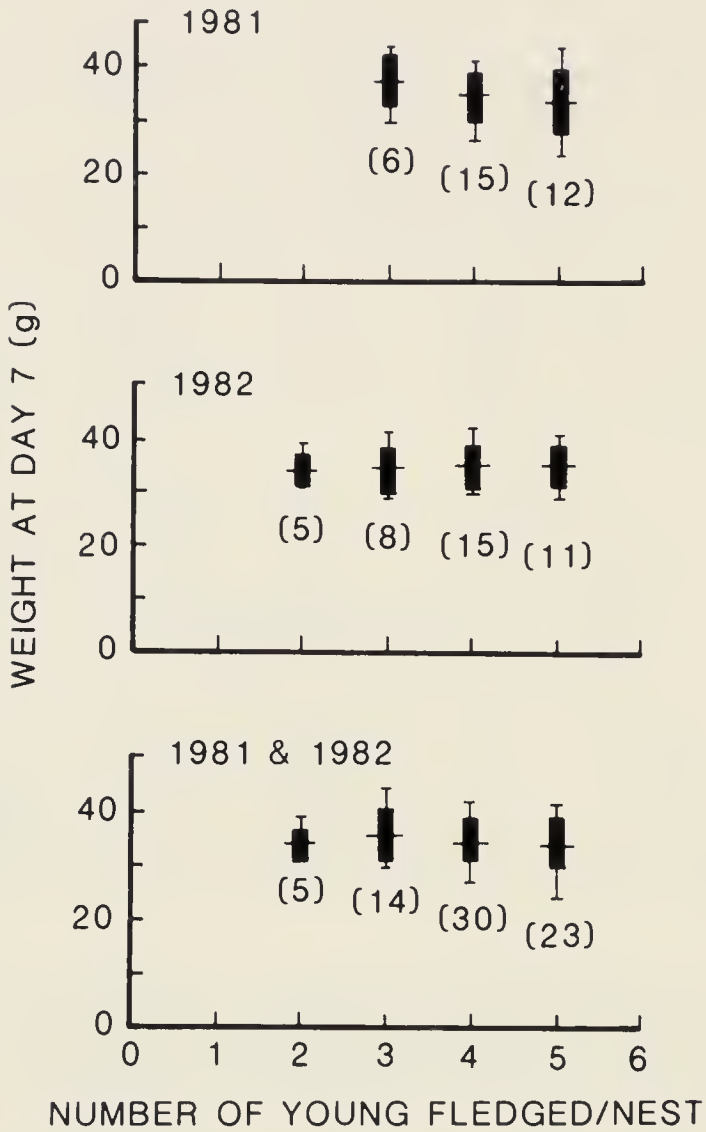


FIG. 3. Growth as a function of the number of young fledged per nest. Numbers in parentheses indicate sample size. Mean, range, and standard deviation are indicated.

Northway population (9 days between first clutch initiation and median clutch initiation) is greater than that observed for other populations in North America. This synchrony may be a result of the synchronous emergence of insects imposed by the short subarctic summer (see Kaufmann 1971).

Mean egg length, breadth, and volume found in this study are larger than those found by other studies (Bent 1958, Crawford 1977, Brown and Goertz 1978). The larger egg size observed for this population may be due to environmental factors. It is possible that females lay both larger and more eggs in response to good foraging conditions in the egg-laying period. Alternatively, larger eggs may be due to larger female body weight. Power (1970) found that 92% of the geographical variation in female

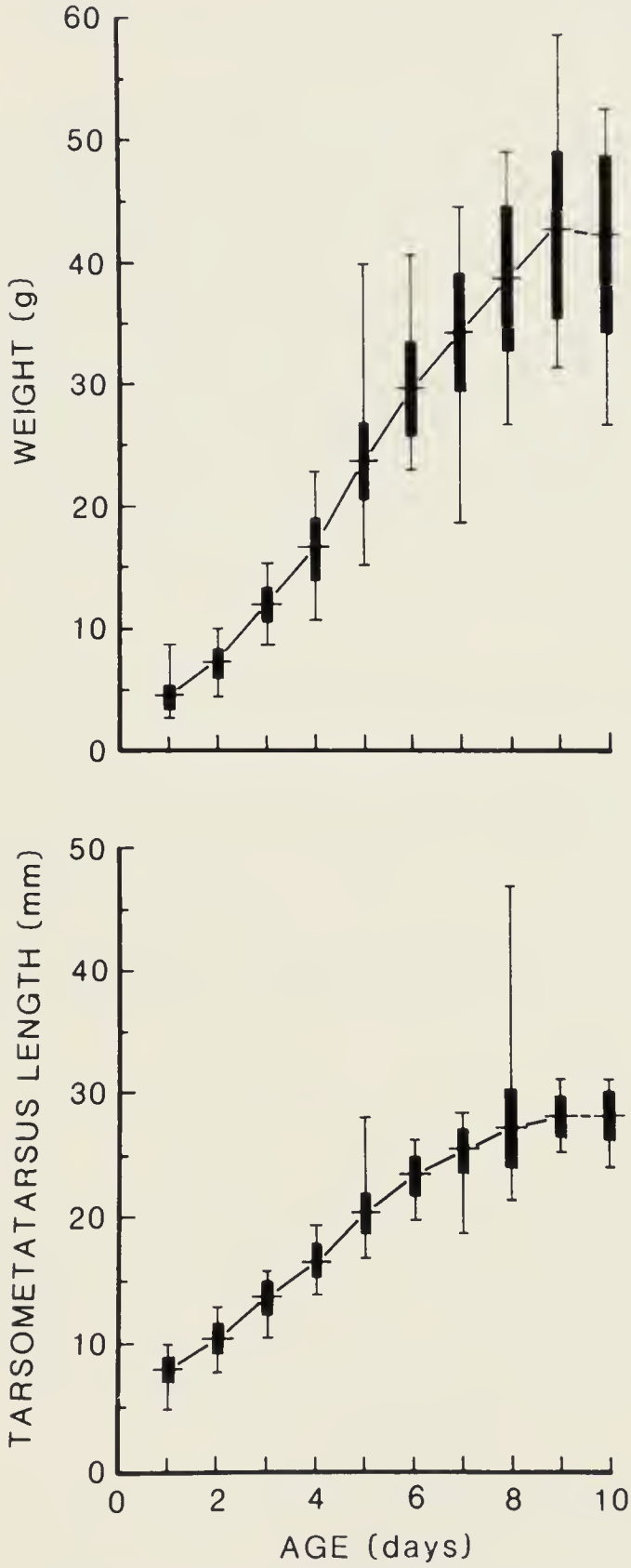


FIG. 4. Nestling weight and tarsometatarsus length as a function of age (1981 and 1982). Mean, range, and standard deviation are indicated.

redwing body weight was attributable to a measure based primarily on latitude.

At fledging (days 9 and 10) the nestlings in the Northway population were heavier than nestlings in the other studies (Williams 1940, Payne 1969, Robertson 1973, Dyer and Abramsky 1976, Crawford 1977, Strehl 1978, Cronmiller and Thompson 1980, Fiala 1981, Fiala and Congdon 1983). Only Cronmiller and Thompson (1980), working on a New York population of redwings, showed a similar magnitude in weight increases during the nestling period. If food were especially abundant during the nestling period, nestlings could gain weight at the maximum possible rate. The observation that nestlings in different size broods are the same weight at day 7 (Fig. 3) suggests that nestlings in the two years of this study gained weight at a rate that is near the physiological maximum. Robertson's (1973) data on tarsometatarsus lengths closely resemble my data, suggesting that growth of tarsometatarsi may be independent of breeding location.

The average clutch size of birds in the Northway population is higher than that found in other studies of Red-winged Blackbirds (e.g., Wood 1928, Orians 1961, Holcomb and Twiest 1968, Miller 1968, Payne 1969, Holcomb 1971, Holm 1973, Blakely 1976, Francis 1976, Crawford 1977, Weatherhead and Robertson 1977, Brown and Goertz 1978, Moulton 1981, Lenington 1982, Rigby 1982). This agrees with Lack's (1968) observation that intraspecific clutch size in passerines increases with latitude. It is not clear, however, if larger clutches reflect a genetic difference between this population and populations farther south, or whether females could be laying larger clutches because of good foraging conditions prior to and during egg laying.

In my study, both hatching success and fledging success are much higher than those reported in other studies over the range of the Red-winged Blackbird (e.g., Perkins 1928, Wood 1928, Smith 1943, Brenner 1966, Goddard and Board 1967, Miller 1968, Robertson 1972, Caccamise 1976, Francis 1976, Brown and Goertz 1978, Payne 1979, Rigby 1982). Lack of predation, low interspecific competition, abundant food, and mostly warm sunny weather during the nestling period in both years of my study may, in part, account for the high nesting success.

## ACKNOWLEDGMENTS

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research, and S. F. MacLean, Jr., who initially stimulated my interest in evolution and ecology.

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# AGE-SPECIFIC FORAGING ABILITY AND THE EVOLUTION OF DEFERRED BREEDING IN THREE SPECIES OF GULLS

ALEXIS A. E. MACLEAN[1]

ABSTRACT.—From 1976 to 1978, I studied the foraging performances of all age classes of the Bonaparte's Gull (*Larus philadelphia*), the Ring-billed Gull (*L. delawarensis*), and the Herring Gull (*L. argentatus*). In all species, immatures foraged less efficiently than did adults. There was improvement in performance with age, the adult level of efficiency being achieved in the spring of the final year of adolescence. A correlation was established between the extent of performance depression in the immatures and the length of the species-specific prereproductive period. Search, pursuit-capture, and handling improved at different rates and in different sequences in the three species. Implications for deferred breeding are discussed. *Received 25 May 1984, accepted 20 Sept. 1985.*

Central to the discussion of deferred breeding is the fact that reproductive activities carry both benefits and costs. The benefits include genetic representation in future generations. The costs have been defined as "any decrement in either the effectiveness of another function or in the probability of surviving to perform that function, or both" (Williams 1966). Recent theoretical treatment of deferred breeding by Goodman (1974), Wittenberger (1979), and Stearns and Crandall (1981), among others, has demonstrated that deferred breeding will be favored only when the benefits, expressed as increments in the lifetime production of offspring, exceed the costs of forfeiting one or more years of potential reproductive output.

Of the various theories proposed to account for the presence of greater cost factors in immatures, the most widely accepted is that proposed by Ashmole (1963), who suggested that young lack certain of the skills required for their own maintenance and, hence, survival. He further suggested that these skills were acquired gradually, through experience, and that until these skills were perfected, the young birds, as a class, would exhibit elevated mortality relative to that of adults. Ashmole specifically mentioned foraging ability as one such skill. A number of studies have since confirmed that young of gulls exhibiting deferred breeding do indeed forage less efficiently than do their conspecific adults (Searcy 1978, Burger 1981), but none of the studies has attempted to correlate the extent of foraging inefficiency or the rate of foraging improvement with the length

[1] Dept. Biology, Bishop's Univ., Lennoxville, Québec J1M 1Z7, Canada.

of the period through which breeding is deferred. If, as Ashmole suggests, the acquisition of certain skills influences the age at which breeding commences, then the rate at which these skills are acquired should be correlated with the speed with which reproductive activities are assumed.

I studied the foraging behavior of all recognizable age classes within three species of gulls: the Bonaparte's Gull (*Larus philadelphia*) the Ring-billed Gull (*L. delawarensis*), and the Herring Gull (*L. argentatus*), birds that breed for the first time when they are two, three, and four year of age, respectively. I sought to answer the following questions: (1) Do immatures of each species forage less efficiently than do adults? (2) Is there any evidence, within each species, of an improvement in foraging ability with age? (3) Is there any correlation between the extent to which foraging performance is depressed in the immature and the length of the period through which immatures defer breeding?

## METHODS

The study was conducted along a 2-km stretch of the Niagara River that flows past Queenston, Ontario, Canada (43°10′N, 79°04′W).

Preliminary studies to determine the suitability of the region were conducted between October 1975 and March 1976. Formal observations were conducted in September–November, 1976 and 1977, and March and April, 1977 and 1978. On each day, observations began at 05:00 h and ceased at 17:00 h.

Foraging success was recorded for all age classes of all species on each day of observation. Individual birds were selected haphazardly, identified as to species and age (using plumage characteristics), and observed continuously thereafter with 10 × 40 binoculars. No data were recorded until the bird was seen to capture and consume a prey. As soon as a bird that had consumed its food resumed flying, a stopwatch was engaged and all behavioral patterns observed were recorded into a tape recorder. Observation and data collection ceased when the bird next consumed prey.

Only behavioral patterns involved in "independent foraging" (Table 1) are included in this paper. Piracy, while important, (and especially prevalent in the Ring-billed and Herring gulls), is not discussed here, but rather in a separate paper (MacLean, in press). Prey taken included fish, insects, and edible "garbage" that the birds took from the water.

A census of the foraging population was conducted twice daily; first at 05:00 h, and again at 12:00 h. Each age class of each species was censused separately. Each census represents the numbers of birds that crossed a visual plane drawn across the study area during a one-min interval.

Data analysis involved the use of nonparametric tests. The data presented in this paper are combined for each age class in each season. Although performance did vary with such parameters as wind speed, presence of rain or snow, sunny or overcast skies, etc., the variance in performance caused by these factors did not differ between adult and immature classes and hence the data were lumped for the purposes of presentation (though not for statistical analysis). Further details may be found in MacLean (1982).

## RESULTS

*Inefficiency of immatures.*—Immature age classes of all species required more time than did conspecific adults to capture and consume prey, at

TABLE 1

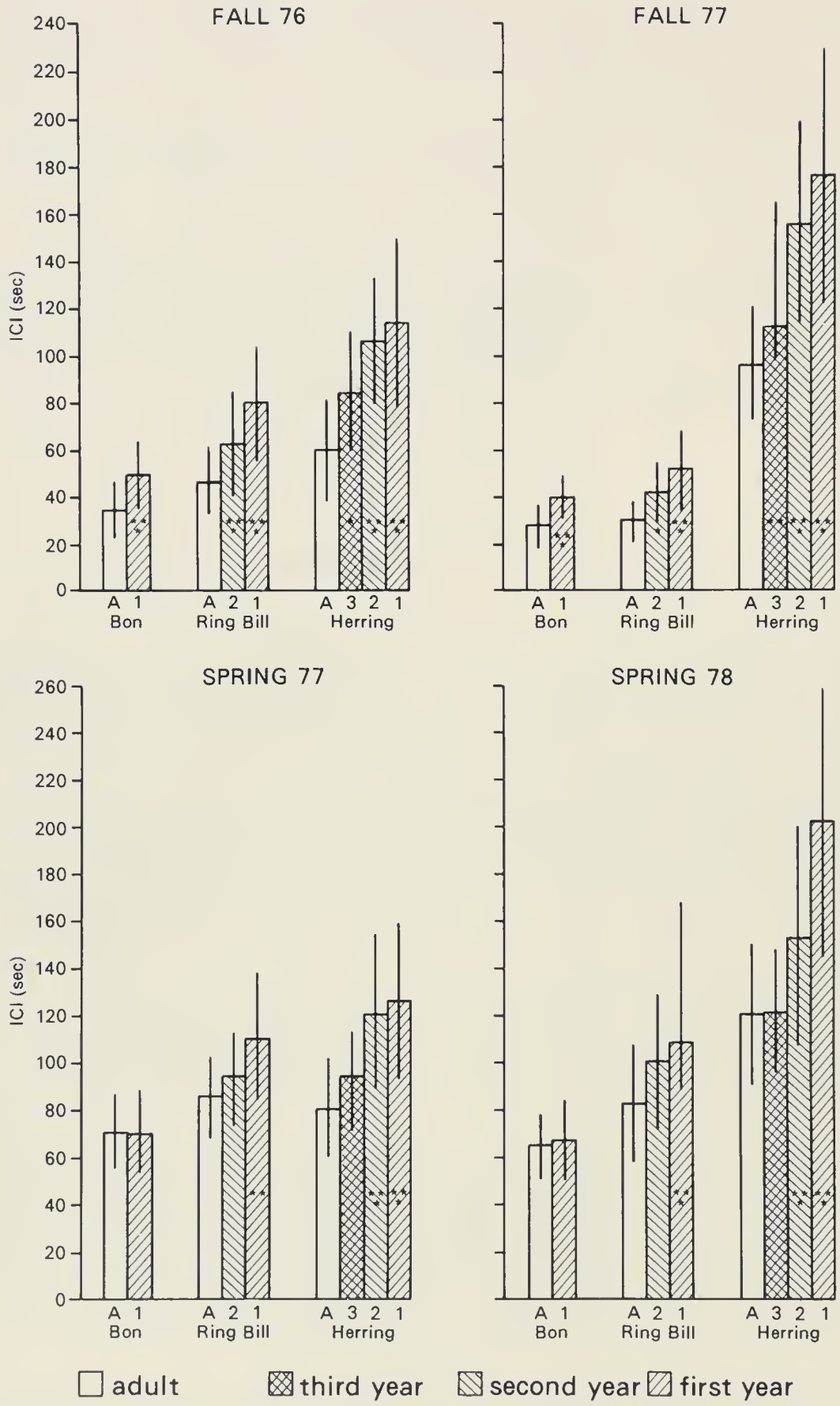
BEHAVIORAL PATTERNS OF FORAGING BONAPARTE'S, RING-BILLED, AND HERRING GULLS

| Behavioral patterns | |
|---|---|
| Dives | Any entry into the water, other than sitting, of any part of the bird. |
| Unsuccessful dive | A dive that did not result in the capture of prey. |
| Successful dive | A dive in which prey was captured and consumed. |
| Drops | Loss of a prey item after capture. |
| Intention movements | Dives that were terminated prior to contact with the water. Termination of the dive occurred at any distance above the water line. No prey was captured. |
| Intercatch interval (ICI) | The time between one successful dive and the next successful dive. |
| Diving rate | The number of dives performed by an individual per unit time. |
| Capture efficiency | The percentage of dives performed that resulted in the capture of a prey item. |

least during fall of each year (Fig. 1). In both fall seasons, the difference between adult and first-year immature performances was highly significant in all three species ($P < 0.001$). The older immature classes of both Ring-billed and Herring gulls also had significantly longer intercatch intervals (ICIs) than did conspecific adults. The pattern that emerged, however, was of a gradual improvement in ability. Second-year Ring-billed Gulls (R2), for example, although less efficient than the adult (RA), were, nevertheless, more efficient than the first-year birds (R1) in both fall seasons. Similarly, in Herring Gulls, third-year birds (H3) were less efficient than the adults (HA), but more efficient than second-year birds (H2), which, in turn, were more efficient than first-year birds (H1). All differences between age classes in each species were statistically significant.

This pattern changed somewhat in spring. Although in spring the ICIs of all age classes were greater than those seen in fall (probably a consequence of reduced fish densities and of the ice cover on the river, which effectively shielded many prey and thereby increased search time) the performance of each immature age class relative to adults improved (Fig. 2). In all three species, all immature age classes improved their performances significantly ($P < 0.05$) between fall and spring, with the oldest immature classes (the R2 and H3) achieving a level of performance that was not statistically different from that of adults.

Thus, in all three species the immatures took significantly more time than did their conspecific adults to capture and consume each prey item, and in each there was a gradual reduction in the average ICI over time.


FALL 76
FALL 77
SPRING 77
SPRING 78
ICI (sec)
A 1
Bon
A 2 1
Ring Bill
A 3 2 1
Herring
adult
third year
second year
first year

The rate of this improvement varied, however, among the three species (Fig. 2, Table 2). For example, in fall, the ICI for the immature Bonaparte's Gulls (BI) was 41% longer than that of the adults. By spring, the two age classes were performing at the same level of efficiency. First-year Ring-billed Gulls (R1), in contrast, had both a greater initial disadvantage (the R1 ICI for fall of 1976 was 70% longer than that of adult birds) and a slower rate of improvement, having achieved only 59% of the reduction in the ICI required to attain the adult level of success. The data for the Herring Gulls indicate even greater initial disparities and slower improvement (Table 2).

*Sources of inefficiency.*—In fall, the immatures of all three species made fewer dives per unit time than did the adults, although the older age classes were relatively more proficient than the younger age classes (Table 3). During fall the immatures also made significantly more intention movements than did the adults (Table 3). The lower diving rates indicate that the young birds of all species do not detect potential prey as readily as do the adults. The data on intention movements (representing as they do terminated dives) indicate that the young birds make more "mistakes" either in the identification of suitable prey or in judging the accessibility of those prey.

In all three species, older age classes of immatures dove more frequently and aborted fewer dives than did younger age classes. As was the case with the ICI, the rate at which this occurred varied among the species, with immature Bonaparte's Gulls improving most rapidly and immature Herring Gulls improving least rapidly (Table 2).

In addition to taking more time and effort in the search for suitable prey, immatures of all species were significantly less efficient than conspecific adults in the capture of prey once these had been found (Fig. 3). In fall, immature classes captured fewer prey per attempt than did adults, and there was gradual improvement in the efficiency of young birds from year to year. All of these increases were significant except for the fall–spring data for R1 in 1977–1978. Performance levels were most depressed in the Herring Gull, the species exhibiting the longest period of immaturity, and least depressed in the Bonaparte's Gull, the species with the shortest adolescence. There are, however, exceptions to this general pat-

←

FIG. 1. Intercatch interval (ICI) for three species of gulls. Bars indicate average ICI for each age class, vertical lines indicate ± 1 SD. Asterisks indicate level of significance for adult-immature comparisons: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

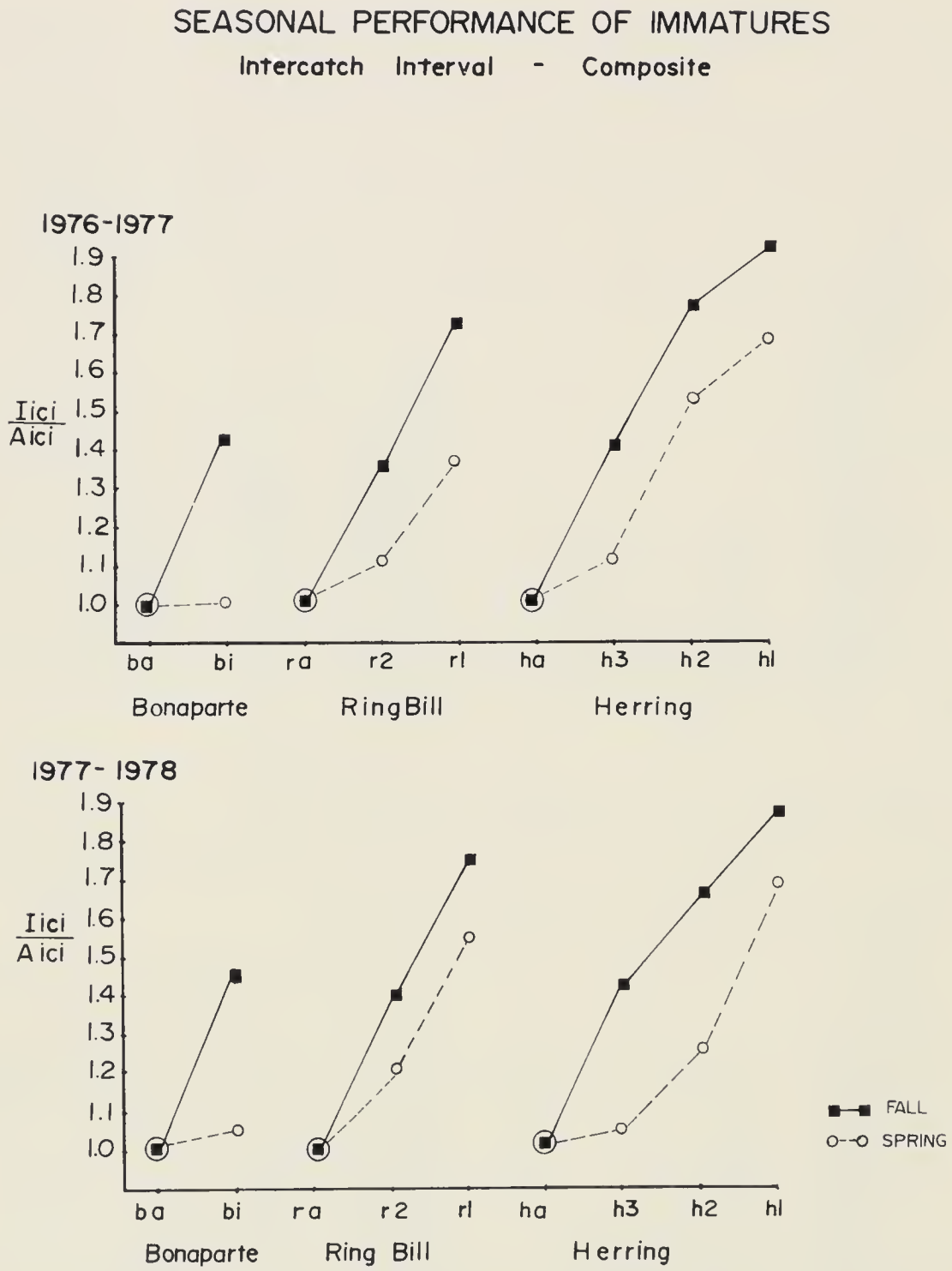



FIG. 2. Intercatch interval (ICI) data for all three species of gulls. Immature performance in a season is expressed as a percentage of the adult performance observed during that same season. Species-age abbreviations as in text.

tern. For example, the relationship between the performances of the first-year Ring-billed and Herring gulls (R1 and H1) is far from clear-cut. In some seasons the relative performance of the R1 is better than that of the H1 (spring 1977); in others it is essentially comparable (fall 1977), and

TABLE 2
SEASONAL IMPROVEMENT OF FIRST-YEAR IMMATURES

| Parameter | Year | % reduction needed to attain adult level | | |
|---|---|---|---|---|
| | | Bonaparte's | Ring-billed | Herring |
| Intercatch interval | 1976–77 | 100 | 59 | 38 |
| | 1977–78 | 100 | 24 | 17 |
| Diving rate | 1976–77 | 100 | 68 | 19 |
| | 1977–78 | 100 | 15 | 0 |

in others it is actually worse (fall 1976, spring 1978). Generally, the discrepancy seems to lie with the performance of the first-year Herring Gulls during 1977–1978 when that age class had a relatively high capture rate.

Handling abilities also varied between immatures and adults (Fig. 4). In all three species the young dropped significantly more prey than did the adults. Improvement in handling ability occurred later in adolescence than did ICI and capture efficiency.

*Foraging period.*—Immatures of all three species compensated for their reduced food intake by foraging for longer periods each day (Table 4). The typical adult pattern was to forage intensively in the morning and again prior to sunset, spending the afternoon resting on a nearby hydroelectric plant roof. Immatures, too, followed this pattern, but their morning feeding bout was extended relative to that of adults, and the rest period was foreshortened. For example, in fall 1976, 1514 adult Bonaparte's Gulls were counted during the morning censuses, but only 288 birds of this class were observed during the noon count. That is, only 19% of the morning flock continued to forage at noon. Extended searches of the surrounding area did not reveal a disproportionate number of these birds foraging elsewhere. In contrast, 44% of the immature Bonaparte's Gulls noted during the morning count were still present and feeding in the study area during the noon census. Similar figures were obtained for immature age classes of the other two species.

## DISCUSSION

My observations demonstrate that immatures of three species of gulls forage less efficiently than do adults during at least some portion of each year. They further indicate that foraging performance improves gradually in all species, with the adult level of performance being achieved only by the spring of the final year of adolescence. Similar adult-immature discrepancies have been noted in other studies (Greig et al. 1983). The

TABLE 3

DIVING RATES AND INTENTION MOVEMENTS OF BONAPARTE'S, RING-BILLED, AND HERRING GULLS

| Season | Parameter | Type gull | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | BA | BI | RA | R2 | R1 | HA | H3 | H2 | H1 |
| Fall 1976 | Dives/min | 2.24 | 2.21 | 1.79 | 1.59 | 1.35[b] | 1.25 | 0.98[b] | 0.95[b] | 0.93[b] |
| | Intentions/capture | 0.74 | 1.01 | 0.81 | 0.92 | 1.03[b] | 0.75 | 0.95[b] | 1.02[b] | 1.56[c] |
| Spring 1977 | Dives/min | 0.98 | 1.04 | 0.75 | 0.74 | 0.69 | 0.86 | 0.78 | 0.65[a] | 0.68[a] |
| | Intentions/capture | 0.94 | 1.04 | 0.53 | 0.60 | 1.11[c] | 0.64 | 0.68 | 0.96[b] | 1.71[c] |
| Fall 1977 | Dives/min | 2.20 | 1.79[b] | 2.19 | 1.82[a] | 1.63[b] | 0.70 | 0.54[b] | 0.53[b] | 0.50[b] |
| | Intentions/capture | 0.28 | 0.42[a] | 0.70 | 0.84[a] | 0.95[a] | 0.85 | 1.16[b] | 1.50[c] | 1.90[c] |
| Spring 1978 | Dives/min | 0.96 | 1.01 | 0.83 | 0.74 | 0.65[a] | 0.64 | 0.64 | 0.52 | 0.45[a] |
| | Intentions/capture | 0.97 | 1.01 | 1.00 | 1.00 | 1.35[b] | 0.82 | 0.97[a] | 1.53[c] | 2.13[c] |

[a] Significant difference ($P < 0.05$) between adults and immatures.
[b] Significant difference ($P < 0.01$) between adults and immatures.
[c] Significant difference ($P < 0.001$) between adults and immatures.

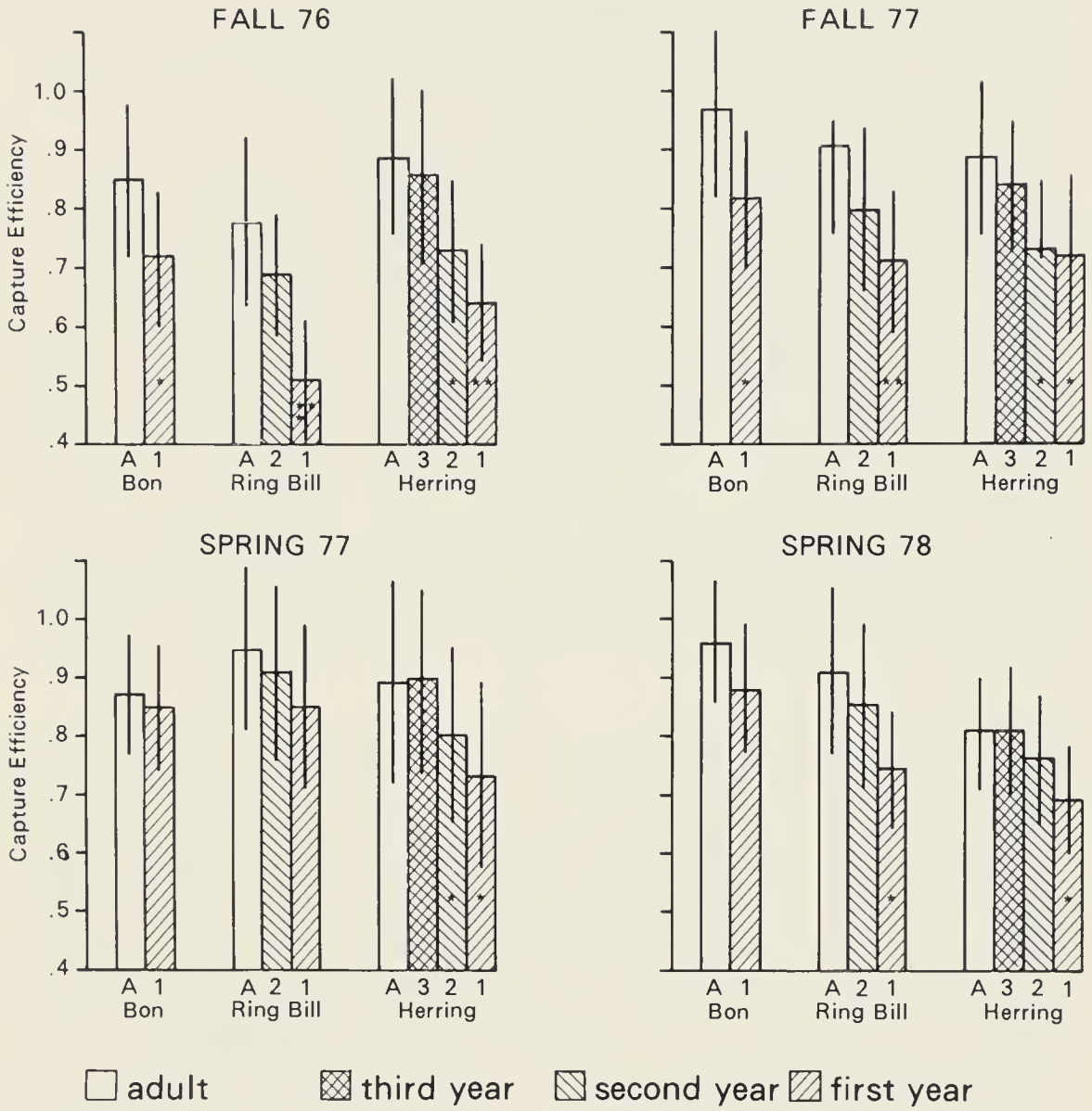



FIG. 3. Capture efficiency in three species of gulls. Bars represent average performance for each age class, vertical lines through bars represent standard deviation. Asterisks indicate level of significance for adult-immature comparisons: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

tendency for young birds to forage for longer periods than do adults has been noted by Schreiber (1968), Spaans (1971), and Davis (1975). Additionally, young have been shown to be less successful pirates than adults (Schnell et al. 1983; Carroll and Cramer 1985). The evidence thus seems overwhelming that such differential efficiency does exist and may contribute, as Ashmole (1963) suggested, to the postponement of breeding. Before the latter connection can be made, however, it is necessary to demonstrate not only the presence of inefficiency in immatures, but also

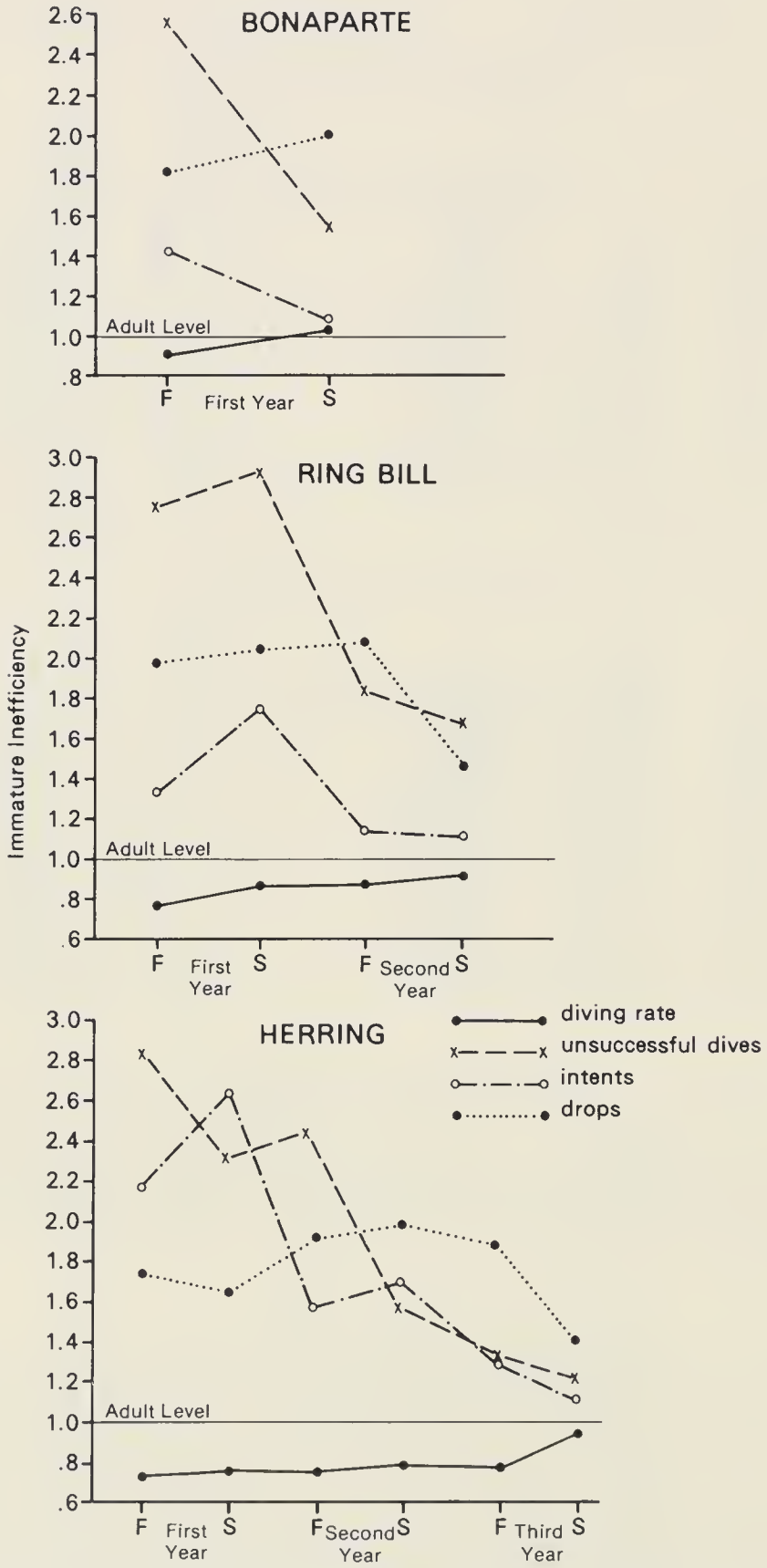



FIG. 4. Summary of various parameters of foraging ability. Immature inefficiency is calculated as the ratio of immature performance to adult performance. F = fall performances, S = spring performances.

TABLE 4

NUMBERS OF BONAPARTE'S, RING-BILLED, AND HERRING GULLS FEEDING ON THE STUDY SITE

| Type gull | Fall 1976 | | Spring 1977 | | Fall 1977 | | Spring 1978 | |
|---|---|---|---|---|---|---|---|---|
| | Morning[a] | Noon | Morning | Noon | Morning | Noon | Morning | Noon |
| BA | 1514 | 288 (19)[b] | 2282 | 342 (15) | 2311 | 208 (9) | 2198 | 132 (6) |
| BI | 458 | 201 (44) | 848 | 263 (31) | 203 | 69 (34) | 202 | 48 (24) |
| RA | 1376 | 220 (16) | 648 | 58 (9) | 812 | 106 (13) | 328 | 33 (10) |
| R2 | 256 | 87 (34) | 150 | 50 (33) | 314 | 63 (20) | 171 | 26 (15) |
| R1 | 562 | 253 (45) | 170 | 68 (40) | 310 | 118 (38) | 236 | 76 (32) |
| HA | 466 | 56 (12) | 232 | 32 (14) | 352 | 35 (10) | 359 | 57 (16) |
| H3 | 148 | 30 (20) | 120 | 25 (21) | 92 | 16 (17) | 103 | 25 (24) |
| H2 | 204 | 59 (29) | 168 | 54 (32) | 120 | 42 (35) | 177 | 71 (40) |
| H1 | 230 | 113 (49) | 244 | 117 (48) | 140 | 73 (52) | 222 | 122 (55) |

[a] Counts represent numbers of birds foraging in the study area during morning (05:00) and noon (12:00) on each day of observation. All comparisons between morning and noon counts within an age class are significant ($P < 0.001$).

[b] The percent of the morning flock foraging during the noon census.

that the extent of foraging inefficiency in the young is correlated to the length of the period during which these birds defer breeding. The data I collected indicate such a correlation. For example, in terms of capture rate, as one passed from Bonaparte's to Ring-billed to Herring gulls, the relative efficiency of the first-year birds declined from 59% to 30% to 10% during fall 1976, and the rate of improvement in performance was most rapid in the Bonaparte's Gull and least rapid in the Herring Gull.

One might also ask whether the species differ not only in the *rate* at which their foraging abilities improve but also in the *ways* in which their foraging abilities improve. That is, given that the immatures of all three species improve their foraging abilities with time (albeit at significantly different rates), is the mechanism for improvement the same in all species? What is being improved, and when?

Searching ability improves abruptly in the Bonaparte's Gull, occurs at a fairly even pace throughout immaturity in the Ring-billed Gull, and is restricted primarily to the final year of immaturity in the Herring Gull (Fig. 4). Similar, and even more marked, differences among species are evident in the "pursuit-capture" component of foraging behavior (Fig. 4). Young Bonaparte's Gulls improved their searching abilities (diving rate), while simultaneously improving their pursuit-capture abilities, as indicated by the decrease in both the numbers of unsuccessful dives and intention movements performed. This was not the case in either Ring-billed or Herring gulls. In the Ring-billed Gull there appears to be a stepwise improvement in abilities (Fig. 4). First, the searching ability (diving

rate) improved. But, while this resulted in the young bird locating more prey than it had previously done, it lost more prey than previously as a result of inefficient pursuit and capture, as illustrated by the increase in both unsuccessful dives and intention movements during the first year. The pursuit-capture abilities of the young Ring-billed Gulls began to improve only during their second year. Handling ability improved even later during the second year (Fig. 4).

In the Herring Gull the pursuit-capture component of foraging performance improved first (Fig. 4). The number of unsuccessful dives was reduced as the number of intention movements increased. The birds were apparently catching their mistakes earlier in the diving sequence. Thereafter, both intention movements and unsuccessful dives declined in frequency. Handling ability (prey dropped) improved most slowly; the improvement was noticeable only during the final year of adolescence. Improved searching abilities were primarily restricted to the older immature classes (H2 and H3), although there was some improvement earlier.

It would thus appear that young gulls improve their overall foraging performance not only at different rates but also in somewhat different ways. In the Bonaparte's Gull, search and pursuit improve simultaneously; handling ability only improves later. In the Ring-billed Gull, searching ability improves first, pursuit and capture abilities next, and handling ability last. In the Herring Gull, pursuit improves first, and handling and searching abilities second. In future studies it may be beneficial to examine not only the presence or absence of immature foraging inefficiencies, but also the sequence in which the various aspects of foraging behavior are improved. This type of information, previously noted in only a few studies (e.g., Bildstein 1983, 1984), together with data on rates of improvement, might then allow us to understand better the determinants of the length of the prereproductive period.

## ACKNOWLEDGMENTS

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# THE EFFECTS OF MUSCLE BIOPSY ON SURVIVAL AND CONDITION IN WHITE-THROATED SPARROWS

DAVID F. WESTNEAT[1]

ABSTRACT.—Baker's (1981) muscle biopsy technique has not been used widely for electrophoretic studies of free-living birds because of initial concern over its effect on bird behavior and survivorship. In this study, I report recapture rates, fat deposits, mass, and return rates between years for biopsied and control White-throated Sparrows (*Zonotrichia albicollis*) wintering in North Carolina. Biopsied birds were recaptured significantly more than controls in one of the two seasons. I discuss the possible effect of slight initial differences in weight on recapture rates. Comparison of changes in fat deposits of biopsied and control sparrows revealed no significant differences in either year. Biopsied birds in 1984 lost significantly less body mass than controls (0.00 g vs 0.56 g). There was no significant difference in return rates between years for biopsied and control birds. Biopsies do not appear to affect survival or condition in this migratory songbird. *Received 3 May 1985, accepted 24 Oct. 1985.*

Electrophoresis is a useful technique in long-term studies of behavior as related to genotypes (Sherman 1981), yet its potential has not been realized completely, as most electrophoretic studies have resulted in sacrificing the studied animal. In several recent studies (Gowaty and Karlin 1984, Mumme et al. 1985, Gavin and Bollinger 1985) blood samples from live subjects were analyzed by electrophoresis for comparison with behavioral observations. The results of these studies were limited, however, by the small number of polymorphic loci found in blood. Several other techniques for sampling tissues of living birds have been published. One of these, the pectoralis muscle biopsy of Baker (1981), gives more resolvable genetic loci than samples of blood or feather pulp (Marsden and May 1984) and, unlike the feather pulp method, can be used without recapture throughout the year. The method, however, does result in an open wound in the main flight muscle, and concern over its effect on birds is justified.

Here, I report on a study of the effects of muscle biopsy on survival and condition in wintering White-throated Sparrows (*Zonotrichia albicollis*).

## MATERIALS AND METHODS

White-throated Sparrows winter in large numbers at the Mason Farm Biological Reserve of the University of North Carolina in Chapel Hill, North Carolina. During the months of

[1] Dept. Biology, Univ. North Carolina, Chapel Hill, North Carolina 27514.

November to February in 1982–83, 1983–84, and 1984–85, sparrows were captured, individually color banded with plastic split-bands, sexed, aged, measured, and released at the point of capture as part of a study on the relationship between social dominance and genetics. The birds were captured in seed-baited Potter treadle-traps distributed along 300–400 m of rose hedges and field edge. In 1982–83, 10 sites with 3–7 Potter traps at each were spaced roughly 40 m apart along 300 m of hedgerow, and in 1983–84 the trapline was expanded to 16 sites, spaced exactly 25 m apart, with 6 traps at each site.

In March of 1983 and 1984, birds caught along the same 100 m of trapline (3 sites and 18 traps in 1983, 5 sites and 30 traps in 1984) were biopsied and released at point of capture. Observations of dominance were performed at two locations along the trapline. To avoid influencing the dominance relationships at one of these locations, all of the birds I biopsied were captured near the other location. There were no differences in the sex ratios or age distributions at the two locations (W. Piper, pers. comm.). Birds caught and biopsied weighed slightly but significantly less than control birds. This difference should make a test for the effects of biopsy more conservative.

In 1983, birds captured at the remaining traps were used as controls. In 1984, because the trapline was longer, the traps for biopsied birds were located in the interior of the trapline. To calculate recapture rates of controls, I used only birds captured at 36 traps (6 sites) similarly located in the interior of the trapline, and birds captured at several traps at either end of the trapline were not considered in these analyses.

For the biopsy I followed Baker's (1981) procedure, except that I used a suture of black silk thread to close the incision. Approximately 0.02 g of muscle was removed from each bird. Birds were held in the hand with the wings between the first and second fingers and the head pointing toward the wrist. I removed a piece of the surface layer of pectoralis muscle (2 mm wide × 8 mm long × 1 mm deep) with iris dissection scissors. In 1983, the birds were biopsied in the field at the site of capture; biopsies were taken 5–30 min after capture, and birds were released immediately after suturing. In 1984, biopsies were completed at a banding station within one h of capture, and the birds were released 10–50 min later at the site of capture. In both years, control birds were measured at the site of capture and released within one min.

Birds in both groups were scored for deposits of fat in the furcula and on the abdomen. Observers scored fat blindly with respect to the state of the birds except when a biopsy had recently (0–7 days) been performed. In these cases a scab could be seen by the observer when scoring fat. Furcular fat was scored from 0 to 4 using the procedure of Helms and Drury (1960). Abdomen fat was scored as follows: 0 = no fat, 1 = less fat visible than muscle, 2 = fat coverage roughly equal to muscle, 3 = more fat than muscle, and 4 = abdomen completely covered with fat. Individuals were given composite scores of the furcula score plus the abdomen score. In 1984, birds were weighed before biopsy with one of three calibrated Pesola scales.

Trapping and biopsies occurred during a span of four and six weeks in 1983 and 1984, respectively. Birds captured for the first time after two weeks were not considered for the within-season analyses. Recaptured birds were recorded, remeasured, and released. Biopsy wounds were checked and the rate of healing noted.

Birds that returned between years were either trapped or observed at feeding platforms. In all years, the intensity of trapping and observations was uniformly distributed along the trapline, and trapping of control and biopsied birds occurred simultaneously.

I tested for differences in return rates within each year and between years with a Chi-square analysis. Biopsied and nonbiopsied birds were compared with Mann-Whitney $U$-tests for differences in fat scores between initial capture and first recapture. A two-tailed $t$-test was used for the comparison of body mass.

## RESULTS

In 1983, 41 White-throated Sparrows were biopsied, and 67 individuals captured and released as controls; in 1984 there were 76 biopsied and 68 control birds. All biopsied birds flew normally on release. Examination of the biopsy wounds of recaptured individuals indicated that the wound formed a scab within a day and was difficult to see in 7–14 days. The suture appeared to facilitate the healing process, primarily by pulling the skin over the wound in the muscle. All birds recaptured after the wound had healed had lost the suture. Birds recaptured up to a year later all had a slight depression in the muscle and a small amount of scar tissue.

The behavior of the birds was not noticeably affected by the biopsy. In 1984, observations of dominance continued after some of the birds had been biopsied, and in no case did the biopsy affect a bird's rank (W. Piper, pers. comm.). Additionally, although some individuals began migrating during this time, both control and biopsied sparrows were still present into May (W. Piper, pers. comm.).

I analyzed the major effects of muscle biopsy by comparing recapture rates of biopsied and control birds under the assumption that biopsy would affect the birds within seven days. In 1983, 66% of the biopsied birds and 52% of the control birds were recaptured after six days ($\chi^2 = 1.92$, df = 1, $P > 0.20$). In 1984, however, significantly more biopsied than control birds were recaptured after six days (59% vs 34%, $\chi^2 = 5.48$, df = 1, $P < 0.02$). No differences between the two groups were found in the number of days elapsing until recapture in 1983 ($\chi^2 = 2.44$, df = 2, $P > 0.25$) or in 1984 ($\chi^2 = 0.57$, df = 3, $P > 0.90$). In 1983, no birds were recaptured in the two days after initial capture, and in 1984 less than a third were recaught on the day after initial capture.

Birds in both groups in both years lost fat during the interim between initial capture and recapture. A Mann-Whitney *U*-test of the differences in changes in fat between initial capture and first recapture for biopsied and control birds was not significant in either year (1983, $z = 0.10$, $P > 0.45$; 1984, $z = 0.93$, $P > 0.17$) (Table 1). The power of this test against the alternative that biopsy actually caused the loss of one unit of fat was 0.97 in 1983 and was 0.84 in 1984.

Control birds lost significantly more mass than did biopsied birds (0.56 ± 0.84 [about 2% of total body mass] vs 0.00 ± 1.17, two-tailed *t*-test, $t = 2.06$, df = 77, $P < 0.05$).

In both years biopsied birds returned to the study area the following year at the same rate as did control birds (1983, 40.4% vs 31.2%, $\chi^2 = 1.26$, df = 1, $P > 0.25$; 1984, 41.0% vs 47.0%, $\chi^2 = 0.35$, df = 1, $P > 0.70$).

TABLE 1
CUMULATIVE (FURCULA PLUS ABDOMEN) FAT SCORES FOR BIOPSIED AND CONTROL WHITE-THROATED SPARROWS

| | 1983 | | 1984 | |
|---|---|---|---|---|
| | Initial capture | Recapture | Initial capture | Recapture |
| Biopsied | 4.3[a] (41)[b] | 2.9 (26) | 3.5 (76) | 2.7 (63) |
| Control | 4.5 (66) | 3.0 (32) | 3.1 (69) | 3.0 (35) |

[a] See text for explanation of fat scores.
[b] Number of birds.

## DISCUSSION

One possible explanation for why more biopsied birds than controls were recaptured is that biopsies might have prevented birds from initiating migration. If control birds in good condition left the study area while those in poor condition stayed, then the remaining birds would be biased toward birds in poor condition. In 1984, however, those control birds that stayed did not have significantly greater mass on initial capture than those birds that were not recaptured (two-tailed $t$-test, $t = 1.72$, df = 28, $P > 0.05$). In addition, the return rates between years suggest that biopsied birds had no more difficulty in preparing for and completing a migration of over 1000 miles round-trip (Chapel Hill, North Carolina, to southern Canada) than the controls.

A possible explanation as to why biopsied birds lost less weight than controls is a difference in time elapsing before first recapture between biopsied and control birds (cf. Mueller and Berger 1966). In the present study, however, there was no difference between the biopsied and control groups in days elapsed until recapture in either year.

Differences between biopsied and control birds in recapture rate and weight loss might have resulted from systematic initial differences between controls and biopsied birds. The recaptures in the two months preceding the 1984 biopsies showed a trend for birds caught in the traps designated for biopsies to be recaptured more frequently in the short run. Also, comparison of masses of all biopsied and control birds on initial capture revealed that biopsied birds averaged 1.3 g less than controls, a highly significant difference (two-tailed $t$-test, $t = 3.25$, df = 103, $P < 0.002$). This result suggests that differences existing before biopsy might have caused the higher short-term recapture rate of the biopsied birds.

My results indicate that biopsies do not affect condition or survival of wintering White-throated Sparrows. If biopsied birds were in poorer condition initially, then the biopsy should have had an even greater effect on

these individuals. Biopsies, however, did not impair these birds' ability to maintain fat deposits and mass or to survive the rigors of migration.

Biopsies may affect birds of other species and at other times of year more severely. In a study of breeding Indigo Buntings (*Passerina cyanea*), in collaboration with R. B. Payne and S. Doehlert (Westneat et al. 1986), I found no adverse effects on the condition of breeding males, nesting females, and nestlings. Resighting rates and return rates between seasons did not differ between biopsied and control birds except for nestlings. However, when Frederick (1985) used this technique on 3 White Ibises (*Eudocimus albus*) (2 females, 1 male) that were rearing young nestlings, none of the birds was seen again. Ibises have a completely feathered breast, and incisions resulted in far more bleeding than in passerines.

Recently, Mumme et al. (1985) remarked that the low degree of variability in blood samples from Acorn Woodpeckers (*Melanerpes formicivorus*) severely limited the results of their study. Considerably more loci can be resolved from muscle tissue than blood or feather pulp (Marsden and May 1984). Additional loci will not make parental assignment substantially easier, but they will increase the probability of excluding a putative parent if it is not the actual parent.

Although caution is required in the study of details of population dynamics, the present study shows that long-term study of genetics and behavior is possible without measurable harm to the subjects.

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# GENERAL NOTES

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**Distribution of food within broods of Barn Swallows.**—The delivery of food by parent birds and its distribution among nestlings of a brood are important determinants of nestling survival. Despite the role of parental distribution of food among nestlings in the process of brood reduction and subsequent evaluations of fitness, direct observations of parent-offspring interactions in the nest are rare (Löhrl 1968, Best 1977, Rydén and Bengtsson 1980, Reed 1981). Field observations have shown that older and larger nestlings are more likely to survive than are their smaller siblings (Howe 1976, O'Connor 1978a, Richter 1982). This could result from parents selectively feeding larger nestlings (Ricklefs 1965, Dawkins 1976) or from the superior competitive abilities of larger nestlings (Löhrl 1968, Richter 1984). Clearly, both processes can operate simultaneously.

If parent birds are capable of preferentially feeding some nestlings, then they must be able to distinguish among the nestlings of their brood. Such perceptual capabilities are in stark contrast to what many species seem to possess; for example, consider the inability of many passerines to distinguish Brown-headed Cowbird (*Molothrus ater*) and other social parasitic nestlings from their own offspring (Rothstein 1982). Beecher and his co-workers (Beecher et al. 1981a, b; Stoddard and Beecher 1983) have shown that in colonial Cliff (*Hirundo pyrrhonota*) and Bank (*Riparia riparia*) swallows, parental recognition of individual young occurs when the young are mobile enough to intermingle. Individually distinctive "signature calls" develop in chicks at about 15 days posthatch. Their observations show that the subtle differences among conspecific nestlings in the nest are unnoticed by parents.

Internestling competition is aggressive in raptors (O'Connor 1978b, Stinson 1979) but relatively passive in passerines (Skutch 1976). Within a passerine brood, larger nestlings can gape higher and command more favorable positions within the nest than their smaller siblings (Löhrl 1968, Rydén and Bengtsson 1980). A size differential among nestlings often results in the early death of the smallest nestlings (Richter 1984); however, the size of a nestling is not always correlated with the proportion of feedings it receives. For instance, Best (1977) in Field Sparrows (*Spizella pusilla*) and Reed (1981) in Song Sparrows (*Melospiza melodia*) determined that the sequence of feedings was essentially random. Rydén and Bengtsson (1980) observed that increased begging rates and movement toward favored nest positions enhanced the feeding rate of small nestlings.

*Methods.*—The observations we report on here are of the interactions between parental Barn Swallows (*Hirundo rustica*) and nestlings at six nests, three each in 1980 and 1981. The study was conducted in Jefferson County, Kansas, on the Nelson Environmental Studies Area of the University of Kansas, Lawrence. In previous years, Barn Swallows built their nests on the underside of a loft in a barn on the study area. During the fall of 1979, we cut a 7.6-cm diameter hole through the planks above 13 nests that had been active in the past summer, and then filled the hole with a wooden plug.

Nest contents were checked regularly until the appearance of the first egg, after which checks were made daily. On the first hatch day, the wooden plug was replaced with a glass plate. Nestlings were marked for individual recognition by painting nail polish on their crowns; marks were replaced periodically as needed. The nesting pair was given a day to adjust to the plate before observations began on day one posthatch. We observed the birds' behavior through the glass plate over each nest. Upon our arrival at a nest, parent swallows were momentarily agitated, but quickly habituated to our presence. We did not record data until the birds were calm. We recorded the time of each feeding, which nestlings gaped as the parents arrived at the nest, which nestling was fed, and various nestling behavioral

TABLE 1

PROPORTION OF FEEDINGS GIVEN TO EACH NESTLING AS A FUNCTION OF NESTLING RANK

| Year | Nest number | Nestling rank 1 | 2 | 3 | 4 | 5 | 6 | CI[a] |
|---|---|---|---|---|---|---|---|---|
| 1980 | 1 | 0.35 (200)[b] | 0.37 (212) | 0.27 (154) | | | | (0.29–0.37) |
| | 2 | 0.29 (91) | 0.35 (111) | 0.36 (113) | | | | (0.28–0.38) |
| | 3 | 0.19 (41) | 0.11 (24) | 0.16 (34) | 0.15 (31) | 0.17 (36) | 0.21 (45) | (0.12–0.22) |
| 1981 | 4 | 0.22 (16) | 0.30 (22) | 0.27 (20) | 0.22 (16) | | | (0.15–0.35) |
| | 5 | 0.32 (33) | 0.33 (34) | 0.35 (36) | | | | (0.24–0.42) |
| | 6 | 0.28 (51) | 0.32 (53) | 0.20 (37) | 0.22[c] (40) | | | (0.19–0.31) |

[a] 95% confidence interval around expected random distribution.
[b] Number of feedings.
[c] House Sparrow nestling.

patterns such as preening and defecation. It was impossible to keep track of nestling gaping at Nest 3 in 1980 because it contained six nestlings.

To test parental recognition of nestlings, a House Sparrow (*Passer domesticus*) nestling was added to Nest 6 in 1981 on day two posthatch. Its weight (4.5 g) was equal to that of the lightest Barn Swallow nestling. Two other House Sparrow nestlings were added to two other Barn Swallow nests (not monitored as part of the main study) in 1981 on day nine posthatch and the reaction of the adult and nestling swallows to the intruders noted.

Quantitative data reported here are based on 1450 feedings of the nestlings at the six nests. Nestlings were weighed to the nearest 0.5 g with a 25-g Pesola scale every second or third day beginning within one day of hatch (except Nest 3 where nestlings were first weighed on day four). Weighings were discontinued after day 12–15, as nestlings approached fledging, to avoid causing premature departure from the nest. Weights on other days were estimated by linear extrapolation between known weights; we assumed a constant age-specific growth rate between consecutive weighing days. This approach has been used by Crossner (1977) to estimate parameters of logistic growth curves. For our purposes, we needed only to be able to rank the nestlings by weight. Nest 1 had the greatest weight difference between highest and lowest ranked nestlings (5 g on day three, increasing to a maximum of 10 g on day seven, but reduced to 1 g on day 17). By comparison, the other five nests showed maximum weight differentials of 3.0, 7.5, 2.5, 4.5, and 5.0 g, respectively.

*Results.*—Our main interest was in determining whether the rank of a nestling (where nestlings were ranked by weight) influenced the nestling's probability of receiving food from parents. To that end we addressed the following questions:

(1) Did all nestling ranks receive an equal proportion of the feedings? Because a nestling's rank sometimes changed during the nestling period, the data for a particular rank included

TABLE 2

CORRELATIONS BETWEEN BARN SWALLOW BROOD AGE AND PROPORTION OF DAILY FEEDINGS GIVEN TO NESTLINGS OF HIGHEST AND LOWEST RANK

| Year | Nest number | Nestling rank: Highest | Nestling rank: Lowest |
|---|---|---|---|
| 1980 | 1 | −0.85[a] (12)[b] | 0.70[a] (12) |
| | 2 | 0.07 (10) | −0.19 (10) |
| | 3 | 0.07 (8) | −0.33 (8) |
| 1981 | 4 | −0.76[c] (7) | 0.14 (7) |
| | 5 | −0.30 (11) | 0.63[c] (11) |
| | 6 | 0.16 (9) | −0.09 (9) |

[a] Spearman rank correlation coefficient is significantly different from 0.0 at $P < 0.01$.
[b] Number of days observed.
[c] Spearman rank correlation coefficient is significantly different from 0.0 at $P < 0.05$.

observations from several nestlings. We compared the proportion of total feedings given to each nestling rank against the null hypothesis of an equal distribution to each rank using a $t$-test for proportions (Walpole and Myers 1978). Only for Nest 1 did any of the proportions exceed the approximate 95% confidence interval around the expected random distribution of feedings to all nestling ranks (Table 1). Hence, based solely on total feedings, high rank does not seem to confer an advantage to nestlings.

(2) Does the potential value of high rank change with nestling age? Due to asynchronous hatching, the within-brood coefficient of variation of nestling weight can be high, but it drops for surviving broods as weights of nestlings converge near fledging. Hence, the relative weight difference between the highest and lowest ranked nestlings in a brood usually decreases as nestlings age. To determine whether the significance of high or low rank to feeding probabilities changed with nestling age, we looked at the correlation between nestling age and the proportion of total daily feedings received for the nestlings of highest and lowest rank in each brood. Again at only one nest, Nest 1, does the importance of rank clearly change with age (Table 2). Here, the highest ranked nestling received a high proportion of the feedings at an early age with the lowest ranked receiving progressively more as the brood aged. Similar trends occurred in nests 4 and 5 in 1981.

(3) A nestling has to gape to be fed, but a gape does not guarantee a feeding. Does rank confer an advantage such that a nestling of high rank will be fed a greater proportion of times following a gape than one of low rank? Using ANOVA, we compared the average conditional probability of a nestling being fed given that it gaped (total number of feedings/total number of gapes) among groups of nestlings ranked by weight. To keep the ANOVA balanced, and in order to include all nests where gapes were recorded, only nestlings ranked one through three were compared. To avoid bias due to absolute feeding rate or food abundance differences, proportions were expressed as deviations from the mean for each brood. Even the highest ranking nestling was passed over from 40 to 52% of the times it gaped for food (Table 3). The ANOVA summary shows that the mean probability of a nestling being fed following a gape is different between ranks (Table 3). The standardized group means are similar for ranks one and two, whereas the mean is lower for nestlings of Rank 3 ($\bar{x}_1 = 0.028$, $\bar{x}_2 = 0.033$, $\bar{x}_3 = -0.06$). Hence, there is some indication that, compared to high-ranked individuals, lower-ranked nestlings were less likely to be fed when they gaped.

TABLE 3
PROBABILITY OF A NESTLING BEING FED FOLLOWING A GAPE

| Year | Nest number | Nestling rank[a] 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| 1980 | 1 | 0.57 | 0.45 | 0.32 | |
| | 2 | 0.56 | 0.56 | 0.32 | |
| 1981 | 4 | 0.48 | 0.59 | 0.55 | 0.50 |
| | 5 | 0.60 | 0.68 | 0.60 | |
| | 6 | 0.49 | 0.52 | 0.37 | 0.43[b] |

[a] Difference among ranks 1 to 3 is significant by ANOVA at $P < 0.01$; Mean Square Ranks/Mean Square Error = 0.0379/0.00117 = 32.3 = $F_{2,12}$.
[b] House Sparrow nestling.

(4) Can defecation influence feeding probabilities? Even at one day after hatching, each nestling oriented its cloaca toward the outside of the nest prior to defecating. Initially, this facilitated parental removal of the fecal sacs as defecation occurred in the presence of an adult. Later, the nestling defecated over the front of the nest. This turning was very rapid and took place even on top of the other nestlings. Surprisingly, an equally rapid return to a forward-facing position was not observed until nestling day 12. Once oriented to the rear of the nest, the nestlings gradually returned to a forward-facing position, but up to 30 min elapsed before a return was achieved. Whatever the mechanism, the consequence was that, regardless of size, no nestling could maintain an advantageous position in the nest as defecation removed it temporarily from the front of the nest. To determine whether defecation reduced the probability of a nestling being fed, we compared, for each brood, the average probability a nestling would be fed given that it just defecated, to the null hypothesis of a random distribution of feedings. A paired comparison $t$-test was used to compare the two sets of probabilities. The probability of being fed following defecation was significantly lower than the average probability of a feeding (Table 4).

(5) Are House Sparrow nestlings rejected? All three of the House Sparrow nestlings were fed by their foster parents, despite their different appearance, calls, and gaping behavior. Two reached weights (22.5 g and 29.0 g) consistent with expectations for normally fledged House Sparrows in the Lawrence area (Murphy 1977). On four occasions beginning on day seven at Nest 3 and on day 10 and 14 at one of the unmonitored nests, the House Sparrow nestling was found on the ground below the nest. Both nestlings were fed by their foster parents following replacement in the nest.

*Discussion.*—Reed (1981) concluded from his study of a single Song Sparrow brood that although feedings were randomly distributed among nestlings, a dominant nestling could receive a higher proportion of the feedings by maintaining a position in the nest near the parents' arrival point. In his study, nestling position shifted in association with feeding bouts, and no nestling was dominant. Our observations showed that the total distribution of food items to nestling Barn Swallows was generally independent of nestling rank. High rank, however, increased the probability that a nestling would be fed, given that it gaped. In Nest 1, the feedings were not randomly distributed among the nestlings, and the difference was most pronounced at young nestling ages (Table 2).

We found, unlike Reed (1981), that the reordering of nestling position following defecation changed the probability that particular nestlings would be fed. Like Reed (1981), we feel

TABLE 4

EFFECT OF DEFECATION ON FEEDING PROBABLITIES

| Year | Nest number | Mean probability of being fed | Probability of being fed following defecation[a] |
|---|---|---|---|
| 1980 | 1 (46)[b] | 0.33 | 0.22 |
| | 2 (10) | 0.33 | 0.10 |
| | 3 (10) | 0.17 | 0.10 |
| 1981[c] | 4 (9) | 0.25 | 0.22 |
| | 6 (13) | 0.25 | 0.15 |

[a] Average difference between probabilities is significantly different from 0.0, $\bar{d} = 0.128$, $S_d = 0.07$, $t = 4.08$, df = 4, $P < 0.05$.
[b] Number of observed defecations.
[c] No defecations were observed at Nest 5.

that the periodic change of nestling position could result in an even distribution of food to all nestlings in a brood if the nestlings are of about equal weight.

The feeding of the House Sparrow nestlings implies that Barn Swallow parents cannot distinguish their own nestlings from those of a different species. Burtt (1977) showed that Barn Swallow parents distinguish their own offspring from other conspecific young only after fledging. Adults behave aggressively toward alien fledglings that are soliciting feedings. There is good evidence that in colonial swallows parental recognition of nestlings does not occur until chicks are mobile enough to leave the nest (Beecher et al. 1981a, b). Stoddard and Beecher (1983) suggest that individual chick facial patterns may facilitate recognition in the Cliff Swallow. As our nestlings were individually marked for our recognition, they might have appeared distinctive to their parents. Our observations ended prior to fledging, however, and the distribution of feedings did not suggest any within-nest discrimination by parents.

As parent Barn Swallows cannot distinguish among their nestlings, they are not capable of actively manipulating brood size following hatch. Brood-size changes are likely the result of differing competitive abilities among nestlings. Despite the general acceptance of this concept, studies of nestling feeding have found only a weak relationship between nestling size and proportion of feedings received (Best 1977, Rydén and Bengtsson 1980, Reed 1981). However, larger nestlings tend to receive a higher proportion of first feedings and need to gape less for food (Löhrl 1968, Rydén and Bengtsson 1980). In times of food shortage, larger nestlings may force the starvation of their smaller siblings, but this has yet to be demonstrated empirically.

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W. BRUCE MCGILLIVRAY AND HOWARD LEVENSON, *Dept. Ornithology, Provincial Museum of Alberta, Edmonton, Alberta T5N 0M6, Canada; and Office of Technology Assessment, Washington, D.C. 20510.* *Received 16 Jan. 1984, accepted 16 Oct. 1985.*

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**Species-area relationship of migrants in isolated woodlots in east-central Illinois.**—Many species of birds use woodlots temporarily for resting and foraging while on migration (Martin 1980, Graber and Graber 1983), and the loss of forest habitat and its fragmentation into isolated patches may adversely affect these birds (Graber and Graber 1983). Isolated patches of forest may be important particularly to migrants in highly disturbed landscapes where

natural habitat is rare (Martin 1980). East-central Illinois is primarily agricultural land that is unsuitable for many forest-dwelling species, although isolated woodlots are refuges for summer residents (Blake and Karr 1984). Because migrating birds encounter and use a variety of habitats during the course of migration, many species may use woodlots that are smaller than they generally require for breeding. Thus, small patches of forest may be more important for species preservation than conclusions drawn from studies of birds during the breeding season might suggest (Blake and Karr 1984).

Here I examine the relationship between area of isolated woodlots in east-central Illinois and number of species found in these woodlots during migration. I emphasize results collected in spring because dense foliage and the relatively inconspicuous behavior and plumage of many species made birds harder to detect in fall.

*Methods.*—A total of 14 woodlots, ranging in size from 1.8 to 600 ha, were studied during spring (1979–1981) and fall (1979–1980) migratory periods. Because of time constraints and adverse weather conditions, I was not able to include all woodlots in each season. Censusing in 1980 was more extensive than in either 1979 or 1981. Number and choice of woodlots were dictated by the landscape of east-central Illinois. Only woodlots that possessed a relatively mature canopy and well-developed understory, showed no evidence of recent heavy disturbance, and were surrounded by nonforest habitat were included.

I surveyed birds using the point-count technique (Ferry and Frochot 1970). Absolute sampling effort (number of observation points) increased with area in order to obtain a reasonably complete count of species present in larger woodlots. Points were at least 150 m apart.

I conducted censuses from sunrise until 2.5 h after sunrise on days with little or no wind and no precipitation. Weather patterns may strongly influence movements of migrants, but I did not attempt to correlate species numbers in individual woodlots with specific weather patterns. I attempted to minimize potential effects of changing weather patterns by sampling on days without storms, high winds, or other unusual weather. In addition, I censused woodlots in an order unrelated to their size, thereby reducing the potential for weather effects on the species-area relationship.

I visited each observation point for 10 min during a census and recorded all birds seen or heard within the canopy. Hawks and American Crows (*Corvus brachyrhynchos*) were excluded because these species regularly ranged far beyond woodlot boundaries. Nocturnal species also were not recorded. Census effort ranged from 4 to 17 days, with a majority of areas censused a total of 12–17 days. I regressed species number against the number of census days for each woodlot to determine the influence of census effort on species richness. Species richness was expressed as the total number of species recorded in a woodlot over an entire season. In addition, I grouped censuses by dates (using natural breaks of two or more days in censusing to define groups) to examine within-season changes in the species-area relationship during the spring and fall of 1980. Each day that a woodlot was censused was used as an estimate of species richness for that woodlot on that day.

I analyzed species composition on the basis of migratory status because this factor has been identified (e.g., Whitcomb et al. 1981) as particularly relevant to the study of the effects of forest fragmentation on bird communities. I assigned species to two major groups: those that breed in Illinois and those that do not (Bohlen 1978, Kendeigh 1982). The former group included permanent residents in Illinois (including all species for which at least some individuals are resident in east-central Illinois throughout the year), long-distance migrants that overwinter in Central and South America, and short-distance migrants that overwinter south of Illinois but north of the tropics. "Woodlot residents" included all species that bred on one or more of the woodlots surveyed in this study (Blake 1983). Species that do not breed in Illinois included long-distance migrants that winter in the tropics and short-distance migrants that either pass through Illinois or are winter residents.

TABLE 1
DISTRIBUTION OF SPECIES RECORDED DURING MIGRATION IN WOODLOTS IN EAST-CENTRAL ILLINOIS

| | | Breeding residents | | | | Transients | |
|---|---|---|---|---|---|---|---|
| Woodlot area (ha) | Total species | Woodlot[a] residents | Permanent residents | Long-distance migrants | Short-distance migrants | Long-distance migrants | Short-distance migrants |
| 1.8 | 45 | 13 | 7 | 11 | 9 | 10 | 8 |
| 2.3 | 58 | 19 | 9 | 12 | 15 | 12 | 10 |
| 4.7[b] | 39 | 19 | 11 | 10 | 8 | 5 | 5 |
| 5.1 | 60 | 20 | 11 | 16 | 13 | 13 | 7 |
| 6.5 | 64 | 22 | 11 | 14 | 14 | 12 | 13 |
| 16.2 | 58 | 18 | 12 | 14 | 13 | 10 | 9 |
| 24 | 67 | 31 | 12 | 15 | 14 | 14 | 12 |
| 24 | 58 | 29 | 10 | 14 | 13 | 12 | 9 |
| 28 | 61 | 36 | 12 | 17 | 14 | 9 | 9 |
| 40[b] | 40 | 22 | 12 | 8 | 8 | 6 | 6 |
| 65 | 64 | 33 | 13 | 16 | 11 | 15 | 9 |
| 65[b] | 54 | 37 | 11 | 18 | 13 | 6 | 6 |
| 118[b] | 54 | 33 | 11 | 17 | 11 | 9 | 6 |
| 600 | 84 | 48 | 13 | 23 | 16 | 16 | 15 |

[a] Includes permanent residents and long- and short-distance migrants that bred on one or more woodlots.
[b] Censused a total of 4 or 5 days.

I evaluated species-area relationships according to the exponential function of Gleason (1922), where $S = k \ln A + c$, where S is number of species, A is forest area (in ha), and k and c are fitted constants. I used the exponential model rather than the power function ($\ln S = z \ln A + \ln c$) because the former model accounted for the greatest amount of variation in species number and because examination of residuals did not indicate that the power function resulted in a better fit. I tested species richness data for normality (Shapiro-Wilks Test, Barr et al. 1979).

*Bird community composition.*—Ninety-five species were recorded from one or more woodlots during one or more seasons. Species totals were highest in 1980 when there was greater coverage of all areas, and totals were higher in spring than in fall, at least in part due to lower detectability of species in fall. Species that breed in Illinois (N = 62) accounted for 65% of the total and included 17 permanent resident species, 30 long-distance migrants, and 15 short-distance migrants. Species that do not breed in Illinois included 18 long-distance and 15 short-distance migrants.

*Species-area relationships.*—Species totals for all seasons combined generally were correlated with number of census days, primarily a consequence of variation in number of transient species. When the four woodlots censused on five or fewer days (Table 1) were excluded, species totals for the remaining 10 woodlots correlated poorly with number of census days. Total species number correlated strongly with area (Species number = 4.8[ln A] + 48.4; $r^2 = 0.719$, $P < 0.01$; N = 10) (Table 1). In addition, number of species in all categories except short-distance migrants was correlated with woodlot area (Fig. 1). Many short-distance migrants preferred edge habitat and were scarce in forest interiors, and they appeared to be less restricted in distribution among woodlots by the area of the woodlot. Number of woodlot residents increased rapidly with area (Fig. 1), but number of permanent

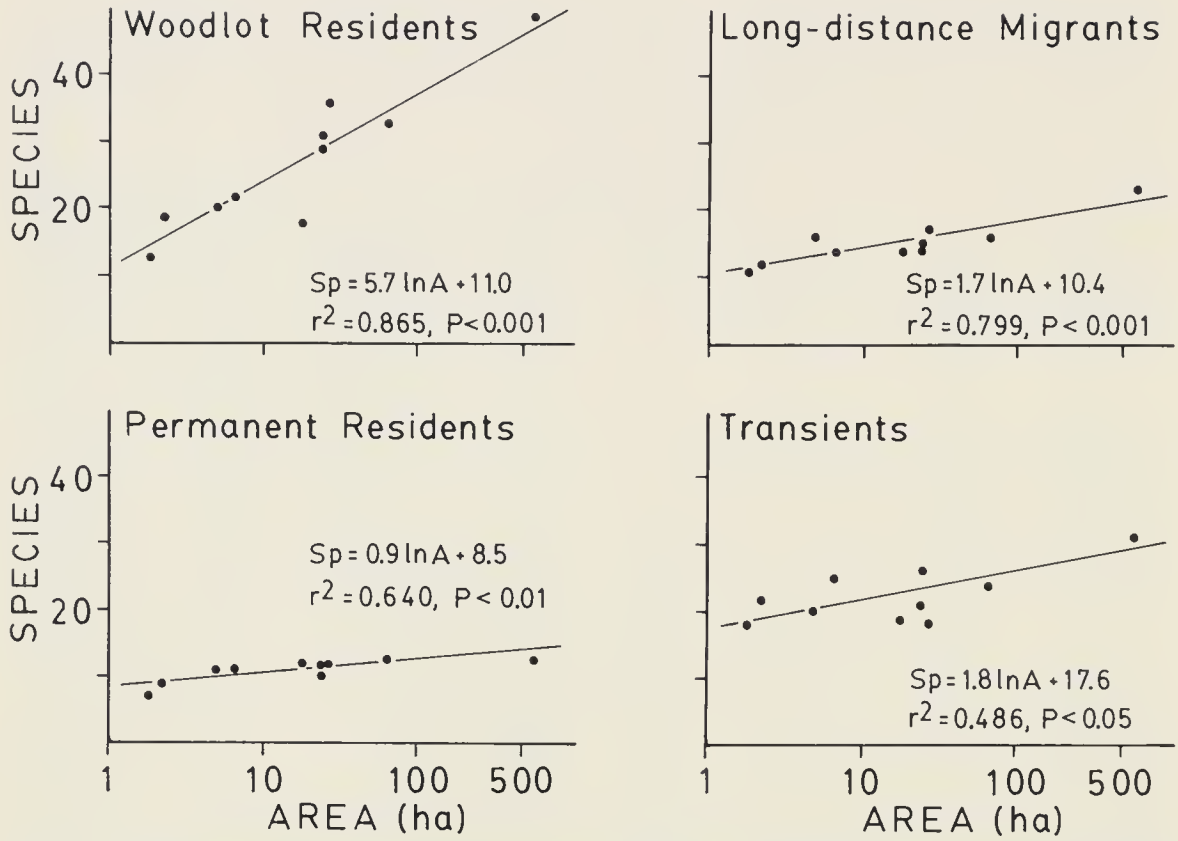


FIG. 1. Species number (Sp) within migratory categories plotted against natural log (ln) of woodlot area (A).

resident species changed little over the size range of woodlots surveyed (Table 1, Fig. 1). Number of transient species was correlated positively with area (Fig. 1), and many species occurred in small woodlots (Table 1).

I examined distribution of species within different migratory categories separately for each season. Total number of species correlated with area in all spring seasons (1979, $r^2 = 0.581$, $P < 0.05$; 1980, $r^2 = 0.745$, $P < 0.001$; 1981, $r^2 = 0.659$, $P < 0.05$) (Fig. 2). Number of woodlot resident species (Blake and Karr 1984) correlated with area in all years as well (1979, $r^2 = 0.755$, $P < 0.01$; 1980, $r^2 = 0.841$, $P < 0.001$; 1981, $r^2 = 0.769$, $P < 0.01$). Number of species of long-distance migrants correlated with area in 1979 ($r^2 = 0.585$, $P < 0.05$) and 1980 ($r^2 = 0.599$, $P < 0.01$), but not in 1981. Many long-distance migrants arrive in Illinois late in spring, a period that was not well covered in 1981 owing to frequent thunderstorms. Number of species that migrate short distances generally correlated poorly with area in all spring periods.

Number of woodlot and permanent resident species correlated with area in fall 1979 ($r^2 = 0.387$, $P < 0.05$ and $r^2 = 0.497$, $P < 0.05$, respectively), but no other group showed a significant correlation with woodlot area in fall 1979. By contrast, all categories exhibited a significant area relationship during fall 1980 when coverage of woodlots was most complete. Correlation between woodlot residents and area was higher during fall 1980 ($r^2 = 0.721$, $P < 0.01$) than in fall 1979, while that for permanent residents was similar to results from 1979. Although number of short-distance migrant species was not correlated with woodlot area in spring 1980, it was in fall 1980 ($r^2 = 0.421$, $P < 0.05$).

Total species richness correlated strongly with area (Fig. 2) during fall 1980. Species totals were lower overall during fall than during spring (Fig. 2), and the species-area relationship

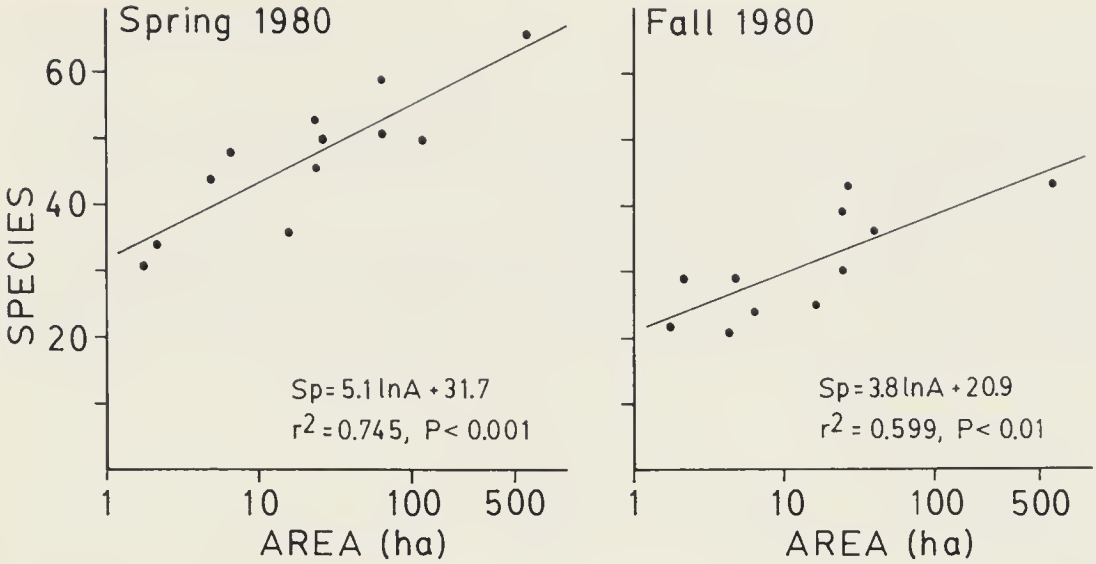


FIG. 2. Total number of species (Sp) recorded during spring and fall migratory periods in 1980 plotted against natural log (ln) of woodlot area (A).

had a higher intercept ($P < 0.05$) in spring than in fall. Slopes of the regression lines, however, did not differ ($P > 0.50$) between spring and fall 1980.

Species richness was correlated significantly with woodlot area in early (16 March–20 April, $r^2 = 0.471$, $P < 0.001$, N = 24) and late (1–31 May, $r^2 = 0.314$, $P < 0.01$, N = 22) spring 1980. The species-area relationship for the later period had a higher intercept (22.3 vs 9.7, $P < 0.001$) than during early spring, but slopes did not differ ($P > 0.10$). Thus the shape of the species-area curve remained constant during spring migration, but species richness increased. During fall 1980, species number correlated most strongly with area during early migration (26 August–10 September, $r^2 = 0.757$, $P < 0.001$, N = 12). During late summer and early fall, many migrating northern warblers pass through east-central Illinois, and the presence of these species influences the species-area relationship. Correlations between number of species and woodlot area were not as strong during middle (14–29 September, $r^2 = 0.234$, NS, N = 13) or late (2–28 October, $r^2 = 0.424$, $P < 0.05$, N = 11) fall migration.

*Discussion.*—Discussions concerning relative benefits of small and large reserves have concentrated on the breeding season (e.g., Simberloff and Abele 1982, Blake and Karr 1984). The relative importance of small forest tracts to birds during nonbreeding seasons can be related to the regional landscape pattern. The ability of migrants to pass successfully over highly disturbed landscapes may be increased by the presence of small patches of natural habitat. Larger woodlots accumulate a greater total number of species, but even small tracts may be used temporarily by a wide variety of species.

Recent studies by Graber and Graber (1983), however, indicate that small woodlots may not be sufficient as refuges for migrants if larger blocks of forest are not available also. Spring warblers were able to put on fat when foraging in southern Illinois, where total forest cover is extensive, but experienced a net energy loss while foraging in isolated woodlots in east-central Illinois (Graber and Graber 1983).

The greater species richness observed in Illinois woodlots during migration over that observed during summer (Blake and Karr 1984) was due both to the arrival of transient species that do not breed in the region and to the occurrence of species in woodlots smaller than those typically required for breeding. Many long-distance migrants (e.g., Ovenbird [*Seiurus aurocapillus*] and other warblers) occurred in a wider size range of woodlots than

during the breeding season (Blake and Karr 1984). Similarly, several permanent residents (e.g., Black-capped Chickadee [*Parus atricapillus*], Tufted Titmouse [*P. bicolor*], White-breasted Nuthatch [*Sitta carolinensis*]) were observed in smaller woodlots during migration than during summer (Blake and Karr 1984). The occurrence of these species in small woodlots during migration suggests that it is not an inability to colonize these woodlots that prevents their breeding in small woodlots during summer.

Many factors, including, but not limited to, high nest predation and parasitism in small forests may limit species occurrence during breeding seasons (e.g., Whitcomb et al. 1981); such restrictions would not apply during migration. Competitive interactions also may limit distribution of species during breeding seasons (Martin 1981), and Martin (1980) has suggested that in very small woodlots (<5 ha) competition may influence distribution of species during migration as well.

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John G. Blake, *Dept. Ecology, Ethology, and Evolution, Univ. Illinois, Champaign, Illinois 68120. (*Present address: *Natural Resources Research Inst., 3151 Miller Trunk Highway, Univ. Minnesota, Duluth, Duluth, Minnesota 55811.)* *Received 8 Oct. 1984, accepted 12 Sept. 1985.*

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**Incubation continuity and the advantage of cryptic egg coloration to Mourning Doves.**—Researchers primarily have addressed two hypothesized functions of egg coloration: (1) that when in direct sunlight, uniformly light-colored eggs are less likely to overheat than are darker eggs because light colors generally reflect solar radiation more efficiently (Montevecchi, Behaviour 58:26–39, 1976a), and (2) that scattered dark spots or scrawls benefit eggs by making them less conspicuous to predators (Lack, Ibis 100:145–166, 1958). Montevecchi (1976a) suggested that these potential functions of egg coloration are opposite selective forces; Bakken et al. (Science 200:321–323, 1978) found that the particular pigments used for cryptic coloration minimize heat absorption from direct insolation.

Little research has been done to document the effectiveness of cryptic egg coloration. Tinbergen et al. (Behaviour 19:74–117, 1962) and Montevecchi (1976a) placed cryptic and white eggs in meadows visited by avian predators and found that cryptic eggs suffered less predation. Bertram and Burger (Ibis 123:207–210, 1981) had similar results when they placed white vs brown Ostrich (*Struthio camelus*) eggs on bare ground. In contrast, Kruijt (Arch. Neerl. Zool. 12:565–567, 1958) found that egg speckling did not reduce predation by Herring Gulls (*Larus argentatus*) on artificial nests. In none of these studies were the eggs attended by adult birds.

Pigeons and doves (Columbidae) are unusual among open-nesting birds because they lay relatively conspicuous eggs of a uniform white or buff color. Columbid parents incubate continually (Kendeigh, Ill. Biol. Monogr. 22, 1952), so selective pressure for egg crypticity probably is weak. White eggs and constant incubation make columbids ideal for studies of egg coloration because a researcher can control both egg color (by painting eggs) and continuity of incubation (by flushing parents from the nest at regular time intervals). Here, we report on a test of the value of cryptic egg coloration to Mourning Doves (*Zenaida macroura*) under regimes of continual vs interrupted incubation. Unlike earlier studies of egg crypticity, our study involved natural nests with parents actively attending them.

*Methods.*—Before we began field work, we tested the effect of brown tempera paint on egg viability by measuring the evaporation rate of Ringed Turtle-Dove (*Streptopelia risoria*) eggs before and after they were spattered with paint. Laboratory results indicated that painting did not affect gas exchange.

Field work was done from May through early August 1983 at Big Creek State Park, Polk County, Iowa. The park contained several km of windbreaks, most of which consisted of a multiflora rose (*Rosa multiflora*) hedge flanked on one or both sides by double rows of jack pine (*Pinus banksiana*) or white pine (*P. strobus*). Most trees were less than 6 m tall, and land between windbreaks was either fallow or used to grow corn, alfalfa, or oats.

We found nests by walking between pine rows and flushing parents. We determined the age of eggs by candling (Hanson and Kossack, Ill. Dept. Conserv. Tech. Bull. 2, 1963). In addition, several nest-site features were recorded: light intensity above the nest (measured with a light meter and expressed as a percentage of ambient light intensity), average nest visiblity from 5 m away (subjectively evaluated on a scale of 1–4 [poor to excellent] from the four cardinal directions), height of vegetation above nest level (tree height minus nest height). Relative light intensity above the nest was used as an index of overhead visibility. Previous analyses indicated that these variables may influence nesting success (Westmoreland and Best, Auk 102:774–780, 1985).

Each nest was assigned randomly to one of four treatments: (1) incubation interrupted and eggs cryptic, (2) incubation interrupted and eggs white, (3) incubation continual and eggs cryptic, and (4) incubation continual and eggs white. Immediately after a nest in treatments 1 or 3 was discovered, eggs were spattered with brown tempera paint (using a

FIG. 1. A clutch of dove eggs before and after being painted.

watercolor brush) to simulate cryptic coloration (Fig. 1). Incubation was interrupted (treatments 1 and 2) by flushing parents from each nest every 3 days. We checked continually incubated nests from about 5 m away (using binoculars) at the same interval, taking care not to approach so closely that the parent flushed. Nest checks in all treatments continued until the nest failed or the eggs hatched.

When a nest was found empty but intact, we attributed the failure to avian predators (Best and Stauffer, Condor 82:149–158, 1980 and references therein). Common Crows (*Corvus brachyrhynchos*) were seen frequently in the area and are known to carry dove-sized eggs away from nests (Montevecchi, Behaviour 57:307–320, 1976b). Mammalian (probably raccoons [*Procyon lotor*] and weasels [*Mustela* spp.]) predation was assumed when the nest was partially or completely destroyed. Snakes and chipmunks (*Tamias striatus*) were seen infrequently in the study area, so predation by them probably was rare. Small nocturnal mammals (mice and shrews) were not considered important predators because one Mourning Dove adult usually is present at the nest overnight. Failures due to factors other than predation (i.e., wind blowing eggs from the nest or nest abandonment) were not included in the analysis.

Incubation was interrupted when nests were initially discovered. Thus, for continually incubated nests (treatments 3 and 4), we eliminated from analysis all data on the interval between nest discovery and the subsequent visit. As a result, comparisons of nesting success between continual and interrupted-incubation regimes are biased and are not discussed here (but see Westmoreland and Best, Auk, 1985). Comparing nesting success between cryptic vs white-egg clutches within each incubation regime, however, was valid. We calculated the daily nest survival probability (Mayfield, Wilson Bull. 87:456–466, 1975) for each treatment and compared them by using one-tailed statistical tests (Hensler and Nichols, Wilson Bull. 93:42–53, 1981). Analysis of variance was used to test for differences in nest-site features among treatments.

*Results.*—We found 130 active nests. One nest failed due to high winds; 12 clutches with cryptic eggs and two clutches of white eggs were abandoned. Eleven of the cryptic-egg abandonments occurred immediately after the eggs were painted; only once did parents initially accept a modified clutch and abandon it later. McClure (Auk 62:270–272, 1945) painted 10 Mourning Dove clutches various bright colors and observed the returning parents; all but one resumed incubation without hesitation. Seven of the cryptic-egg abandonments occurred at nests with interrupted incubation, and the remainder (5) at nests with continual incubation.

Nest-site features (mean vegetation height above nest level = 2.3 ± 0.1 m [SE], treatments pooled; relative light intensity = 19.2 ± 1.5%; nest concealment = 2.8 ± 0.1) and the age

TABLE 1
NEST SUCCESS DATA FOR CLUTCHES OF CRYPTIC VS WHITE EGGS UNDER DIFFERENT INCUBATION REGIMES

| | Incubation interrupted | | Incubation continual | |
|---|---|---|---|---|
| | Cryptic | White | Cryptic | White |
| Number of nests | 29 | 36 | 19 | 31 |
| Number of failures | 8 | 18 | 2 | 7 |
| Daily nest survival probability | 0.957 ± 0.015[a] | 0.915 ± 0.019 | 0.980 ± 0.014 | 0.958 ± 0.016 |
| Estimated success[b] | 54% | 29% | 75% | 55% |

[a] Difference is significant ($P < 0.05$) by Hensler and Nichols (1981) test. Survival probability ± SE.
[b] Based on an incubation period of 14 days (see Mayfield 1975).

of eggs at nest discovery (6.8 ± 0.6 days) did not differ significantly ($P > 0.05$) among treatments. These results suggest that nesting success for treatments was not affected by factors other than egg color and incubation regime.

Cryptic coloration significantly ($P = 0.04$) reduced clutch losses when incubation was interrupted, but did not significantly influence clutch success when incubation was continual (Table 1). Avian predators, probably Common Crows and Common Grackles (*Quiscalus quiscula*), caused 85% of the clutch failures.

*Discussion.*—Our results suggest that cryptic egg coloration has strong adaptive value even when incubation is interrupted infrequently and for short periods. We attempted to determine return times for flushed adults, but were unable to find a method that did not cause abandonment or further increase the risk of predation. Casual observations, however, indicated that birds usually return to the nest within 3 h. McClure (1945) recorded return times of 3–50 min and suggested that most returns are within 1 h.

We found no evidence that Mourning Doves are exposed to selection for egg colors that reduce solar heating. Our cryptically painted clutches were often exposed to incident radiation during adults' absences, but all eggs not taken by predators hatched normally.

Columbid eggs may have originally been cryptic, and lost their color because constant incubation eliminated selection for the trait; conversely, columbids may have evolved constant incubation to cover their white egsgs. We believe that the former is unlikely. Cryptic eggs probably would afford some selective value, even to continually incubating columbids, when parents are flushed from the nest by predators. In our study, survival of cryptic eggs was greater than that for white eggs even when incubation was continual. Although this difference was not significant ($P = 0.15$, Table 1), the hypothesis that cryptic egg coloration is valuable to continually incubating columbids should not be rejected, because the power of the test is low (0.37).

Some aspects of columbid incubation behavior strengthen the notion that continual incubation evolved, at least partially, as a mechanism to reduce the conspicuousness of white eggs. When incubating Mourning Doves are approached, they crouch on the nest and do not flush until almost in contact with the intruder (e.g., Laub, M.S. thesis, The Ohio State Univ., Columbus, Ohio, 1956; Walsberg and Voss-Roberts, Physiol. Zool. 56:88–93, 1983). Brightly colored male Purple-crowned Pigeons (*Ducula spilorrhoa*) also remain on the nest

when approached, but shift positions to keep a patch of cryptic undertail feathers oriented toward intruders (Crome, Emu 75:172–174, 1975).

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**Effects of old nests on nest-site selection in Black-crowned Night-Herons and Snowy Egrets.**—The use of old nests has been reported for Black-crowned Night-Herons (*Nycticorax nycticorax*) (Gross 1923), Little Blue Herons (*Egretta caerulea*) (Burger and Miller 1977), Green-backed Herons (*Buteroides striatus*) (Meyerriecks 1960), Cattle Egrets (*Bubulcus ibis*) and Tricolored Herons (*E. tricolor*) (Jenni 1969); however, the effect of old nests on nest-site selection during the following breeding season has not been investigated quantitatively. Nests of Black-crowned Night-Herons and Snowy Egrets (*E. thula*) survive the winter in large numbers at the Clark's Island heronry, Plymouth, Massachusetts, particularly when they are located in the dense foliage of eastern red cedars (*Juniperus virginiana*). During the spring of 1981 I attempted to determine the effect of old nests on nest-site selection in these two species.

*Study area and methods.*—The Clark's Island heronry (colony 324001, Osborn and Custer 1978) supports a breeding population of 500–600 pairs, mostly Black-crowned Night-Herons and Snowy Egrets (Davis and Parsons 1982).

On 28 March, 43 red cedar trees were divided into a group of 21 experimental trees from which all 52 old nests were removed and the sites of the old nests marked (hereafter "old sites"), and a group of 22 control trees, in which 53 nests were marked but left in place. No herons were observed on the island when the nest removal and tagging were done. All red cedars that contained at least one nest encountered in a transect through the colony were included in the study, and assignment to group was randomized by designating the group in which the next encountered tree would be placed. Nest density was comparable in control and experimental trees. Trees were examined at approximately weekly intervals (Fig. 1) beginning on 18 April, when 2 complete and 11 partial clutches were found. On each visit new eggs were marked, all new nest building noted, and the use of old nests recorded. A nest was considered active if one or more eggs were present. Species was determined by egg size (Snowy Egret eggs are smaller than those of night-herons) and confirmed after hatching. Statistical analysis was by $\chi^2$ tests.

*Results.*—The date of the median active nest for Snowy Egrets was three weeks later than for Black-crowned Night-Herons in both the control and experimental trees (Fig. 1) (median test, $P < 0.05$).

Black-crowned Night-Herons built more nests in control trees than in experimental trees (14 nests/22 trees vs 12 nests/21 trees), as did Snowy Egrets (35 to 24), but the differences were not significant ($P > 0.05$). In control trees, Black-crowned Night-Herons used old nests in 86% of the cases, Snowy Egrets used them 60% of the time (Table 1). In the first nesting in each tree, Black-crowned Night-Herons used old nests in 85% of the cases, Snowy Egrets

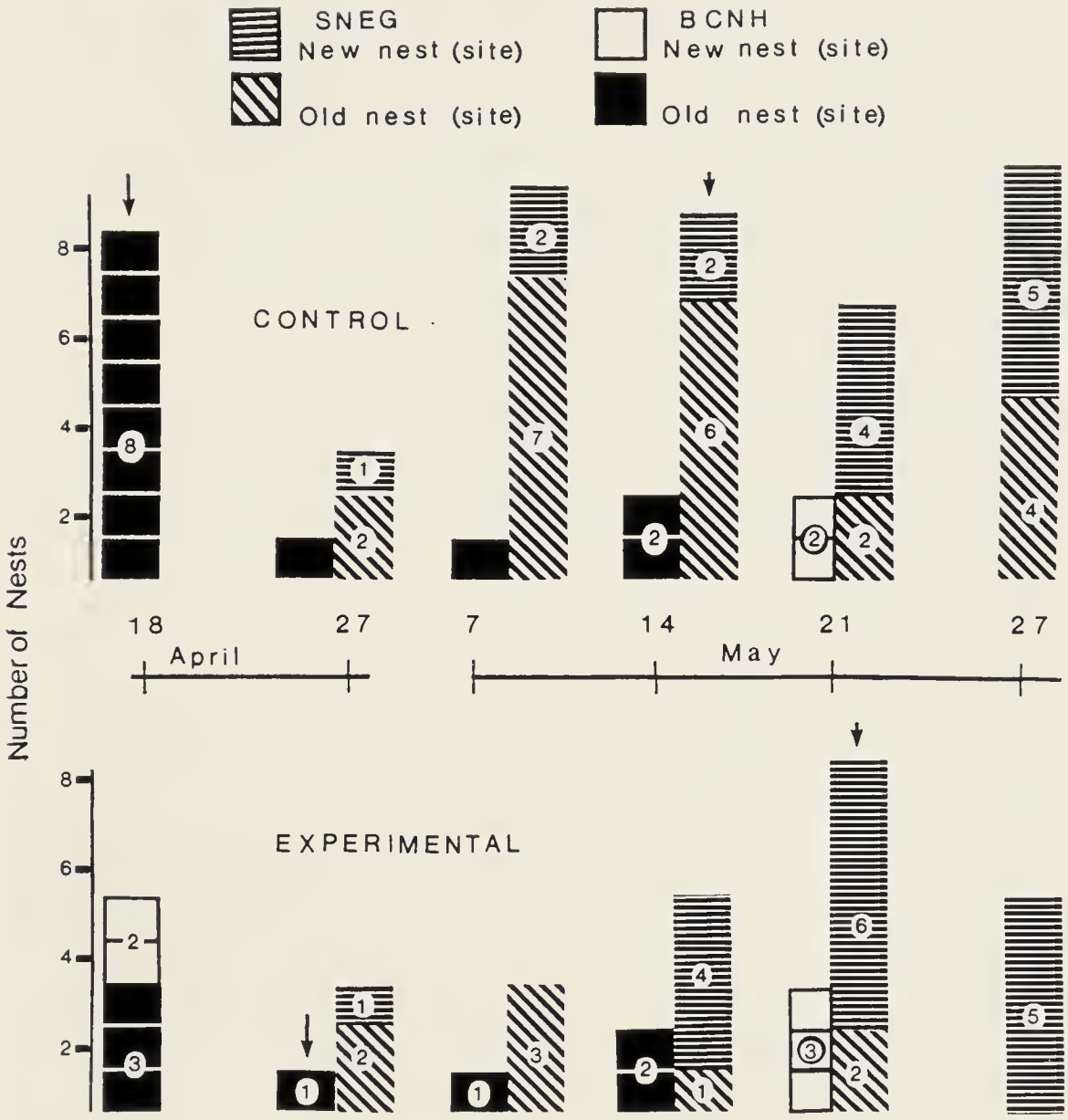


FIG. 1. Nests constructed in control trees (old nests left in place) and experimental trees (old nests removed) in April and May 1981 by Snowy Egrets (SNEG) and Black-crowned Night-Herons (BCNH). Long arrows indicate the date of the median active nest for Black-crowned Night-Herons; short arrows are for Snowy Egrets.

used them 76% of the time. When the data for both species are combined, old nests were used first in 21 of the 22 trees (95%). In the experimental trees, Black-crowned Night-Herons used old sites in 58% of the cases; Snowy Egrets used them 33% of the time. The comparison between the species was not significant ($P > 0.05$).

Both species chose proportionally more old nests in the control trees and old sites in the experimental trees early in the season than late in the season (Fig. 1). For Snowy Egrets, a comparison of the data for weeks of April 27–May 14 (31 nests) with the data of May 21–27 (28 nests), indicates that they chose significantly more ($P < 0.05$) old nests and old sites during the earlier period (15/5 vs 6/9 for old nests; 6/5 vs 2/11 for old sites). Black-crowned

TABLE 1

NUMBER OF SNOWY EGRETS AND BLACK-CROWNED NIGHT-HERON NESTS IN CONTROL AND EXPERIMENTAL TREES, OLD NEST OR NEW NEST CONSTRUCTION (CONTROL TREES), AND NEST CONSTRUCTION IN OLD OR NEW SITES (EXPERIMENTAL TREES)

| | All nests | | | First nest in tree | |
|---|---|---|---|---|---|
| | Old[a] | New | Total | Old | New |
| Snowy Egret | | | | | |
| Control | 21 | 14 | 35 | 13 | 4 |
| Experimental | 8 | 16 | 24 | 7 | 4 |
| Black-crowned Night-Heron | | | | | |
| Control | 12 | 2 | 14 | 11 | 2 |
| Experimental | 7 | 5 | 12 | 6 | 3 |

[a] Old nest in control tree; old nest site in experimental tree.

Night-Herons showed a similar pattern, but small sample sizes (N = 14 in control trees, N = 12 in experimental) precluded statistical comparisons.

Black-crowned Night-Herons had one nest per tree in 21 cases (95%) and more than one nest in 2 trees. Snowy Egrets nested singly in 16 cases (39%) and had more than one nest per tree in 25 trees. Black-crowned Night-Herons had one nest per tree significantly more often than Snowy Egrets ($P < 0.05$).

*Discussion.*—A number of authors have examined factors involved in nest-site selection in herons and ibises. Meyerriecks (1960) suggested that an old nest, if available, was the primary object around which Green-backed Herons center territorial behavior. Burger (1978) suggested that herons selected nest sites on the basis of such characteristics as plant species, vegetation height, and "openness." She also suggested a vertical alignment among species, with the larger herons nesting highest, and with dominance playing an important role. McCrimmon (1978) and Beaver et al. (1980) examined structural nest-site characteristics such as nest height, distance of nest to tree center, and diameter of nest branch, and stressed the importance of vegetation structure in nest dispersion and nest-site selection. Thus both structural characteristics of the nest sites and social factors may play a role in nest-site selection among herons and ibises.

The data presented in this study suggest that nest-site selection by Black-crowned Night-Herons and Snowy Egrets was a complex phenomenon that may have been influenced by (1) the time of nesting, (2) the presence of old nests, and (3) the presence of other nesting pairs.

The date of the median active nest for both species was one week later in the experimental trees. The preference for using an old nest by the first pair of Black-crowned Night-Herons or Snowy Egrets to nest in each tree is consistent with the hypothesis that herons are initially attracted to trees with old nests. As none of the herons or egrets was banded, the possibility that birds returned to the same nest that they had occupied the previous year was not tested.

Both species chose more old sites in the experimental trees early in the season than late in the season, and the difference was significant for Snowy Egrets. The number of available old sites decreased as they were occupied, and it may be that there was a limited number of structurally sound sites in each tree, with the better sites occupied first each year.

Social factors appeared to influence nest-site selection as well, as many Snowy Egrets

nested in trees with conspecifics even though adjacent unoccupied trees were available. Black-crowned Night-Herons are often predators within the colony (T. Custer, pers. comm.), and it may be that the Snowy Egrets gained protection against predation by their social nesting.

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William E. Davis, Jr., *Science Division, College of Basic Studies, Boston Univ., Boston, Massachusetts 02215.* *Received 28 May 1985, accepted 16 Sept. 1985.*

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**The use of tape-recorded calls to count Virginia Rails and Soras.**—Tape recordings have been used for two decades in censusing breeding birds (Johnson et al., pp. 68–75 *in* Ralph and Scott, eds., Studies in Avian Biology, Vol. IV, 1981). Because of the elusive nature of rails and the dense vegetation that they inhabit, tape playing has become a principal means of counting rails. The playing of taped calls significantly increased the calling rate of breeding Virginia Rails (*Rallus limicola*) and Soras (*Porzana carolina*) (Glahn, Wilson Bull. 86:206–214, 1974). Both species responded equally well to interspecific and conspecific calls. Baird (M.S. thesis, Fort Hays State College, Fort Hays, Kansas, 1974), however, found that Soras responded less consistently to taped calls than did Virginia Rails, and concluded that broadcasts of taped calls could not be applied accurately to counting Soras. This paper (1) tests the hypothesis that breeding Virginia Rails and Soras respond equally well to tapes of interspecific and conspecific calls and (2) addresses the value of night counts in obtaining indices of breeding rail densities.

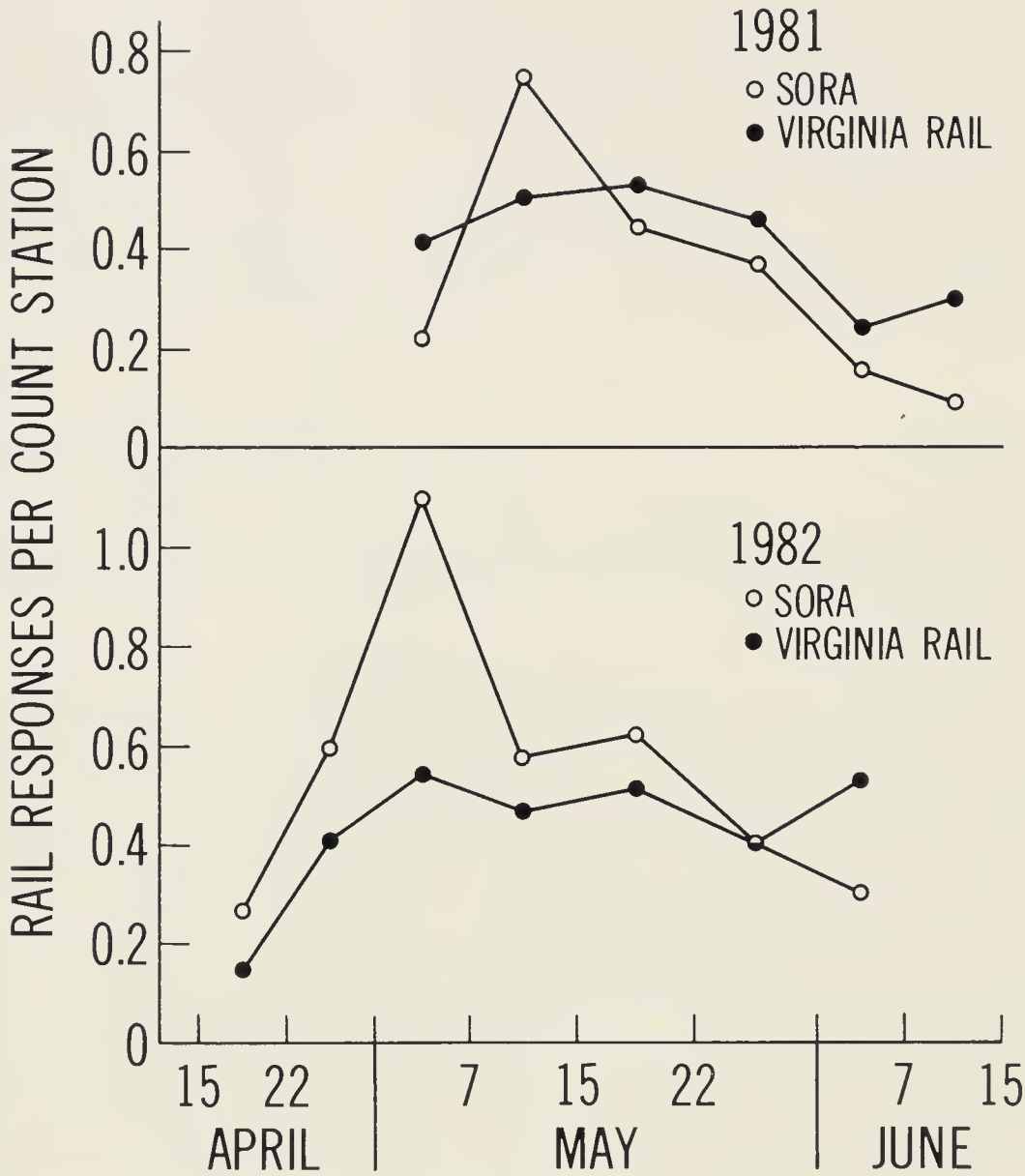


FIG. 1. Weekly response rates of Virginia Rails and Soras to playback recordings per count station during morning surveys in 1981 and 1982.

*Materials and methods.*—We studied the distributions of territorial Virginia Rails and Soras on Dewey's Pasture and Spring Run Game Management Areas, two state-owned wetland complexes in northwestern Iowa. Count routes were established around the periphery of marshes. Along these routes, we established 108 stations at a mean interval of 100 m (30–150 m), thus achieving complete coverage of available habitat. We surveyed 65 ha of wetland, including 52 ha of emergent vegetation. One-minute continuous-loop tapes of the primary advertising call of the Virginia Rail and Sora, each broadcasting seven calls per min, were played with a cassette recorder. Maximum sound pressure one m from the source was 90 db.

We conducted counts between 1 May and 16 June 1981 and 15 April and 1 June 1982. Counts were run at least once per week along each route and were made from 1 h before to 3 h after sunrise. They were not performed when wind velocity exceeded 24 km/h or in

TABLE 1

TAPE RECORDINGS RESPONDED TO BY BREEDING SORAS AND VIRGINIA RAILS IN 1981 AND 1982

| | 1981 No. responding to recordings of | | | | 1982 No. responding to recordings of | | | |
|---|---|---|---|---|---|---|---|---|
| | Sora | Virginia Rail | $\chi^2$ | $P$ | Sora | Virginia Rail | $\chi^2$ | $P$ |
| Sora | | | | | | | | |
| Prelaying | 49 | 16 | 16.8[a] | <0.001 | 130 | 44 | 42.5 | <0.001 |
| Postlaying | 64 | 31 | 11.5 | <0.001 | 92 | 44 | 16.9 | <0.001 |
| Virginia Rail | | | | | | | | |
| Prelaying | 37 | 29 | 1.0 | >0.25 | 49 | 52 | 0.1 | >0.75 |
| Postlaying | 77 | 118 | 8.6 | <0.005 | 65 | 89 | 3.7 | ≥0.05 |

[a] Chi-square test for goodness-of-fit with the expectation of an equal response to recordings of Virginia Rails and Soras.

heavy rain. Night counting was initiated in early June of each year, when morning surveys stimulated few responses to taped calls, and was conducted from 1 to 4 h after sunset.

Virginia Rail and Sora calls were each broadcast continuously for 2 min at each station. The call broadcast first was alternated at each station. For all rail vocal responses, we recorded the tape played first, and the tape responded to, and noted the locations of rails on cover maps prepared from aerial photos. We were conservative in counting responding rails. Unless they were simultaneous, when two responses came from approximately the same location, only one was recorded.

*Results and discussion.*—The responses of 528 Virginia Rails and 470 Soras were recorded. Weekly response patterns for 1982 were similar to those in 1981, but they exhibited an earlier peak in the number of rail responses/station and an earlier decline in response frequency (Fig. 1). This temporal shift reflects differences in nesting phenology. The peak of egg laying occurred approximately 10 days earlier in 1982 (10 May) than in 1981 for both Virginia Rails and Soras.

Soras responding to morning broadcasts were significantly farther away (68 ± 4.4 m [SE], N = 470) than Virginia Rails (51 ± 2.7 m, N = 504) ($t = 2.39$, $P < 0.01$). Virginia Rails responded to night broadcasts (118 ± 7.1 m, N = 124) at a significantly greater distance than during morning counts ($t = 6.84$, $P < 0.001$). During late incubation and brood-rearing, Virginia Rails responded more readily to night broadcasts than to morning broadcasts (0.4 and 0.9 Virginia Rail responses/station, respectively N = 10, $t = 4.2$, $P < 0.001$). Neither morning nor night broadcasts of either Virginia Rail or Sora tapes elicited responses from Soras after early June.

Chi-square analysis of response data indicates that Soras responded to conspecific calls significantly more often than to Virginia Rail calls ($\chi^2 = 98.78$, $P < 0.001$) (Table 1). Virginia Rails exhibited a higher responsiveness to conspecific calls only during the postlaying period ($\chi^2 = 11.70$, $P < 0.001$) (Table 1). Prelaying Virginia Rails exhibited no preference for the calls of either species. The order of tape presentation did not effect the responses of either species.

Our data do not support the hypothesis that Virginia Rails and Soras respond equally well to conspecific and interspecific calls during the breeding season (Glahn 1974). Tacha (M.S. thesis, Fort Hays State College, Fort Hays, Kansas, 1975) found that a large percentage

of Virginia Rail calls were elicited by conspecific calls (78%), while Soras responded best to interspecific broadcasts (71%); however, he had a small sample of Sora responses (N = 17). Our data indicate that where Virginia Rails and Soras are sympatric, both species may be counted successfully during the prelaying period by broadcasting recordings of the Sora's primary advertising call. During the postlaying phase of the breeding season, however, best results are achieved by alternating broadcasting calls of both species.

Night counting seems to be useful for obtaining indices to breeding rail densities. Night counts stimulated greater Virginia Rail response rates, and they responded over a greater radius then than they did during morning surveys. Further investigation is needed to assess the value of night surveys in counting rails during prelaying.

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**Food robbery of wintering Ring-necked Ducks by American Coots.**—Several species of waterfowl (e.g., American Wigeons [*Anas americana*] and Gadwalls [*A. strepera*]) steal food from American Coots (*Fulica americana*) (Munro 1949, Knapton and Knudsen 1978, Ryan 1981), but there are few reports of coots robbing waterfowl. Bent (1926) reported that coots rob Canvasbacks (*Aythya valisineria*) and Redheads (*A. americana*). In this paper we describe observations of coots robbing Ring-necked Ducks (*A. collaris*).

*Study area and methods.*—The study was conducted on Par Pond, an 1120-ha cooling reservoir for nuclear production reactors at the Savannah River Plant, South Carolina. Observations were made between 17 January and 1 April 1985, at three sites (two coves and one open lake site) approximately 3.0 km from one another.

The shallow zones (<2 m) of Kenyon Bay and Loyal's Lair, the two cove sites, were dominated by white water-lily (*Nymphaea odorata*), American lotus (*Nelumbo lutea*), and water-shield (*Brasenia schreberi*). Big-floating bladderwort (*Utricula inflata*) and lemon balm (*Bacopa caroliniana*), shallow water submergents, were also found in both coves. Abundant deep-water (>2 m) submergents included wild celery (*Vallisneria americana*) and Eurasian water milfoil (*Myriophyllum spicatum*). Loyal's Lair contained sparse stands of cattails (*Typha latifolia*) and slender spike rush (*Eleocharis acicularis*), whereas an extensive border stand of cattails and a shallow-water zone of dense spike rush were found in Kenyon Bay. The third site, Cold Dam, had a deep-water zone that was dominated by wild celery. Slender pondweed (*Potamogeton pusillus*) and snailseed pondweed (*P. diversifolius*) were present in the shallow-water zone. Lotus was the dominant floating macrophyte on the site, and cattail was present along the shoreline.

Ring-necked Ducks were selected randomly and observed with a 15–45× spotting scope for 5 min. Approximately equal numbers of males and females were observed. The sex of each Ring-necked Duck robbed was recorded.

Encounters were classified into three categories: (1) direct robbery occurred when a coot took food directly from a Ring-necked Duck's bill, (2) forced food-drop occurred when a coot pursued a surfacing duck and caused it to drop vegetation held in its bill, and (3) scrap-feeding was performed by coots near feeding Ring-necked Ducks that churned up vegetation. Scrap-feeding by coots was recorded as food robbery only when coots fed near Ring-necked Ducks that failed to surface with vegetation. In these instances coots were using a food source that ducks created and were also attempting to consume.

*Results and discussion.*—Thirty-five encounters were recorded at all three sites during 376 5-min periods (31.3 h). All interactions occurred in water less than 2 m deep, where emergent and floating vegetation were common. Eddleman (1983) observed no similar interactions between coots and Ring-necked Ducks in Oklahoma. Male Ring-necked Ducks were robbed more often ($\chi^2 = 19.3$, $P < 0.05$) than were females (18.2% [N = 170] vs 1.9% [N = 206]). We hypothesize males were robbed more often because they shared a more similar feeding niche with coots than did female ducks. Sixty percent (21/35) of the observed encounters took place at the Cold Dam site even though this site held the lowest density of Ring-necked Ducks and coots. Kenyon Bay and Loyal's Lair accounted for 14.3% (5) and 25.7% (9) of the encounters, respectively. We believe that most encounters were observed at the Cold Dam site because of the vegetation available at the site, as coots pursued only Ring-necked Ducks that possessed a narrow-leaved submergent. Although identification was not always possible, the vegetation appeared to be narrow-leaved pondweed (*Potamogeton* spp.).

Only on two occasions did male Ring-necked Ducks respond aggressively to food robbery attempts. In both incidents, the male chased the coots a short distance after surfacing with vegetation in the bill. In both instances, the food was dropped and the coot returned to it while the male Ring-necked Duck resumed feeding.

The most common form of robbery observed was the forced food-drop (62.8%). Ducks did not appear to drop food intentionally when pursued by coots; most attempted to consume the vegetation while fleeing. Direct robbery occurred less often (25.7%), and on three occasions it was observed after most food had been dropped. Scrap-feeding was observed in 42.8% (15) of the encounters, and in all but three cases, it occurred in combination with one of the other food robbery categories. Similar feeding associations have been described for American Coots feeding near Canvasbacks (Anderson 1974), and for Eurasian Coots (*F. atra*) feeding near Pacific Black Ducks (*Anas superciliosa*) and Hardheads (*Aythya australis*) (Woodall 1984).

We believe that the relatively high frequency of food robbery of Ring-necked Ducks by coots on Par Pond can be attributed to different habitat composition and resource distribution in comparison to other areas where coot and waterfowl interactions have been studied.

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JAMES F. BERGAN AND LOREN M. SMITH, *Dept. Range and Wildlife Management, Texas Tech Univ., Lubbock, Texas 79409.* *Received 26 June 1985, accepted 24 Sept. 1985.*

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**Polygyny in the Evening Grosbeak.**—Evening Grosbeaks (*Coccothraustes vespertinus*) are assumed to be exclusively monogamous (e.g., Verner and Willson, Ecology 47:143–147, 1966; Lack, Ecological Adaptations for Breeding Birds, Methuen, London, England, 1968; Terres, The Audubon Society Encyclopedia of North American Birds, Knopf, New York, New York, 1980). Here we present data suggesting that they are at times polygynous. During the summer of 1984 we observed a banded male Evening Grosbeak in two different nesting areas (A and B; about 1.6 km apart) simultaneously associating with two females. Both nests produced young. Observations were made in the Wild Basin area of Allenspark, Colorado (elevation 2591 m), about 80 km northwest of Boulder, Colorado.

Of the two nests, B lagged behind A by about eight days. While female A was incubating, female B was engaged in courtship and nestbuilding. The male sporadically fed female A while she was incubating, but during this period he spent most of his time with female B, courting, guarding her from other males, and participating in nestbuilding. Once young birds were present at nest A, the male spent most of his time feeding them. During this time the male was observed at nest B feeding the incubating female only once, and was not seen there again until the nestlings at B were about 12 days old.

The forest in which these birds lived had a major outbreak of spruce budworm (*Choristoneura fumiferana*) and a minor outbreak of aspen leaf rollers (*C. conflictana*) during summer 1984. Although Evening Grosbeaks are generally assumed to be exclusively monogamous, polygyny may be facilitated when unusually plentiful food and restricted nesting areas influence the "polygyny threshold" (Verner and Willson, 1966; Orians, Am. Nat. 103: 589–603, 1969). In our study area, suitable nesting sites were not restricted. Because polygyny appears to occur very rarely in Evening Grosbeaks regardless of environmental conditions, our observation may be a case of "incidental" polygyny.

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**Nesting trios of Mourning Doves.**—During a 4-year study of reproductive behavior of color-marked Mourning Doves (*Zenaida macroura*) at J. Clark Salyer National Wildlife Refuge in northcentral North Dakota, I observed three cases in which two males and a female attended a nest. Doves were marked with uniquely patterned Saflag wing tags or spray paint on the tail and wings. In an attempt to avoid disruption of pair bonds, I did not mark doves on the head (Frankel and Baskett, J. Wildl. Manage. 27:124–127, 1963; Goforth and Baskett, J. Wildl. Manage. 29:543–553, 1965). Although it is possible that the marking techniques disrupted the pairbonds, this seems unlikely because free-living Mourning Doves marked with back tags have been observed to nest normally (Jackson and Baskett, J. Wildl. Manage. 28:293–307, 1964; Mackey, M.S. thesis, The Ohio State Univ., Columbus, Ohio, 1954). All three adults were color marked at one nest (83-2), both males but not the female were marked at another (81), and only one male was marked at the third (83-1). In each case, there was fighting between the males. These were the only nests in my study where more than two adults were noted; there were monogamous pairs at 485 other nests, most of which included at least one color-marked individual.

I observed each of the three nests from a car 20–40 m away. Nest 81 was observed for 2730 min during 18 observation periods and during 22 spot checks (<5 min duration); nest 83-1 for 135 min during two periods and during 38 spot checks; and nest 83-2 for 4880 min during 33 periods and during 41 spot checks.

*Nest 81.*—On 16 June 1981 I flushed two color-marked males and an unmarked female near an almost completed nest. The first egg was probably laid that night, as all three adults alternately sat on the nest the following day. Male YRO was on the nest when I began observations and remained for 60 min before yielding to male OPO, who incubated for at least 330 min. The female was on the nest at night, as is typical among Mourning Doves (Harris, Morse, and Longley, Am. Midl. Nat. 69:150–172, 1963).

All three birds incubated during the next day: the female for 62 min in late afternoon and again at night, YRO for at least 180 min, and OPO for at least 16 min. In 517 min of observation and during 21 spot checks during the remainder of the incubation period, OPO was not seen on the nest again, although he perched in the nest tree daily, often within 3 m of the nest.

I resumed intensive observations on 2 July, when I first noticed a nestling being fed, and watched birds at the nest for more than 8.5 consecutive hours each day on 2, 3, and 5 July. Again OPO was not seen on the nest although he spent much time in the nest tree and repeatedly approached the nest. Whenever OPO approached, YRO left the nest and flew at OPO until OPO retreated. OPO was usually back in the nest area <1 h after being chased away. The males fought 14 times in 26.2 h of posthatching observation. Fights lasted as long as 10 sec, with the males striking each other with their wings while touching chest-to-chest.

I never saw the female fight with either male. On 18 June the female and OPO engaged in mutual allopreening before she yielded the nest to him. Later, the female pecked at OPO on two occasions when he approached the nest. Once he responded by preening her head, unreciprocated, for 8 min before leaving the area. Mutual allopreening normally takes place between mates (Goodwin, Pigeons and Doves of the World, Cornell Univ. Press, Ithaca, New York, 1983). I never observed allopreening during exchanges at other nests, although Craig (Auk 28:398–407, 1911) noted that allopreening was among the normal activities during nest exchange among captive Mourning Doves.

The nesting attempt failed on 7 July. OPO flushed from near the nest at 06:30. When the

nest was checked at 12:00, no adult was present, and a single nestling (≈4 days old) was dead in the nest. The cause of death and whether it had a nestmate are unknown.

The dominant male (YRO) was not seen again. OPO was seen three more times during the summer. Each time he was alone at times of day when males are generally on their nests (Harris et al. 1963).

*Nest 83-1.*—Only the unbanded male and unmarked female were seen nest-building. The color-marked male (WPP) was first seen in the nest tree on 3 June 1983, the presumed hatching date of the first egg. In 5 of 8 spot checks from 4 to 7 June the unmarked male left the nest to fight with WPP in the nest tree. From 8 to 14 June WPP was not seen during 8 spot checks when either the unmarked male or the female was on the nest.

During both checks on 15 June, WPP was brooding the two large nestlings. One nestling fledged later that day. WPP brooded the other nestling early in the morning and at least twice during the afternoon on 16 June. The second nestling fledged on 17 June. WPP perched next to the empty nest the following morning.

WPP was next seen on 28 June, 5 km from the nest site. He was not seen again until 1984 when he nested 100 m from nest 83-1.

*Nest 83-2.*—The female at this nest (KW) was banded as an adult in 1982. In May 1983 she abandoned her color-marked mate and two eggs that were near hatching (nest 83-0) and copulated with an unbanded male. This unbanded male may have been involved later at nest 83-2, as neither of the males at nest 83-2 was banded until June 1983. Based on the pattern of sightings of KW and one of the 83-2 males (GH), I suspect that this male was mated to KW during nesting attempts in June and July, although neither GH nor KW was observed on a nest during this interval. The other male (BP) was seen frequently between mid-June and late July. His repeated perch-cooing during these sightings suggests that he was unpaired (cf. Jackson and Baskett 1964).

On 2 August 1983 the female (KW) was flushed off nest 83-2. The next day, GH was seen nearby, walking on a lawn at the rapid pace that males generally use while searching for nest materials. When the nest was next checked on 17 August, GH was sitting on the nest and BP was standing on a branch 0.3 m above the nest. On 19 August BP flew into the nest area when GH departed with the eggshell from the second nestling. Upon his return, GH flew at BP who went to a perch 0.7 m away.

The nest was observed for 79 h from 20 August until 1 September, when the young fledged. Beginning 23 August, BP brooded almost three times as much as GH (1538 vs 540 min) and fed the nestlings >3 times as long (49.5 vs 16 min). Each male was in the area and approached the other while it was on the nest. The males fought 14 times. The longest fight lasted 4 min. This fight, involving hard wing flapping, began when GH approached BP on the nest and ended when GH got on the nest. GH initiated 10 fights and apparently "won" 8 of them (i.e., remained on or got on the nest). The female was not involved in any fights.

A radio transmitter was placed on the back of the oldest fledgling, which was observed for 30 h from 5 to 13 September. The only adult seen during these observations was GH who was in the area 5 of 9 days. He flew toward the radio-equipped fledgling and apparently fed it at least once during this time.

*Discussion.*—Nesting trios have not been reported previously in Mourning Doves, although Neff (Condor 47:39–40, 1945) reported that a male Mourning Dove provided parental care at a nest of White-winged Doves (*Z. asiatica*) where the male had disappeared. Mourning Doves with fledged young have been observed to feed fledglings that were not their own (Hitchcock and Mirarchi, J. Wildl. Manage. 49:502–504, 1984; pers. obs.), perhaps because of an inability to recognize their own young.

At each nest that I observed, the relationship between the males was competitive, and the female showed no obvious preference for either. At the two nests where intensive

observations were made, both males spent much time at or near the nest, and I could not determine which male was paired with the female. At all three nests, one male appeared to be unpaired either before or after the nesting. I suspect that these males had temporarily joined in the activities of an established pair. The genetic relationships among individuals were unknown.

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**Supernumerary adults feeding Willow Flycatcher fledglings.**—The Willow Flycatcher (*Empidonax traillii*) maintains a monogamous mating system in which the female builds the nest and broods the young (Verner and Willson, Ornithol. Monogr., 9:1–76, 1969). The male defends the territory and is the primary provider of food at the nest (King, Auk 72: 148–173, 1955). During an intensive ecological study of the Willow Flycatcher in the central Sierra Nevada mountains, Fresno County, California, I observed the previously unreported occurrence of supernumerary adults feeding fledglings.

Individual Willow Flycatchers were captured in mist nets and banded with a unique sequence of four color bands. Each color was assigned a number, resulting in a unique numerical designation for each individual. Early in June 1984, male 0133 paired and mated with female 4110. The relationship between these birds was substantiated by weekly, and at times biweekly, observations throughout the season. Observations during the first week of July suggested nesting, although no nest was found. At 09:40 on 24 July 1984, I observed female 4110 feeding four fledglings. The fledglings were not able to fly more than 15 m, an indication that they had fledged recently.

During subsequent observations, 4110 continued to feed the fledglings. Male 0133 was calling and patrolling territory boundaries and was not observed feeding young. Between 10:40 and 11:00 additional adult Willow Flycatchers and one Dusky Flycatcher (*E. oberholseri*) were observed feeding the fledglings. Dusky Flycatcher 0128 had been banded early in the breeding season and had been noted occasionally at various locations on the study site. Flycatchers 0134 and 0135 had been banded earlier this same day and were believed to be new to the site, and possibly migrants. Flycatchers 0134 and 0135 were considered to be adults based upon complete ossification of the skull and adult wing and culmen length. Furthermore, 0135 exhibited a regressing brood patch indicating that she had recently nested. No aggression was observed between the extra adults and the territory holders.

Two mist nets were subsequently set, one on each side of a large willow (*Salix* sp.), to catch the fledglings. During the 2-h period the nets were open, six adult flycatchers were captured, as well as the four fledglings. The captured included: the female parent 4110;

0128, 0134, 0135, previously noted feeding the fledglings; and two previously unbanded adults now designated 0136 and 0142.

Explanations of supernumerary birds in the vicinity of a nest commonly fall into three categories. Siblings, often from earlier broods or previous years, have been observed feeding young from subsequent broods. Another explanation is that adults that have lost their broods are stimulated to feed gaping young. A third possibility is that adults that are unable to establish breeding territories may comprise a "floater" population in the vicinity of breeding conspecifics. These birds are likewise stimulated to feed gaping young.

The genetic relationships of the birds I observed is unknown except in the case of the obviously unrelated Dusky Flycatcher. As all of the captured birds were adults, it is unlikely that they were siblings or fledglings.

Data collected over two years at two sites in the area suggest that either or both of the remaining explanations may apply. First, not all adults present bred. Some males held territories and never acquired a mate, and adult flycatchers of unknown sex were often observed in the vicinity, suggesting a substantial "floater" population. My observation of a female moving into a territory and nesting late in the season after another female had lost her nest is further evidence of a floater population. At my two sites, only three of eight nests (38%) successfully fledged young; therefore, late in the breeding season, the floater population may include unsuccessful nesters. This is further evidenced by the brood patch of flycatcher 0135.

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**Brood adoption by a male Black-capped Chickadee.**—In species such as the Black-capped Chickadee (*Parus atricapillus*), where males provide extensive parental care, mechanisms that decrease the likelihood of a male raising unrelated young should be selected for. A male that helps raise unrelated young may, however, actually be increasing his expected lifetime reproduction. Odum (Auk 58:314–333, 1941) reported a case where a male Black-capped Chickadee that lost his mate helped raise the nestlings and fledglings of a female that had lost her mate. These two birds then raised a second brood, which he fathered. In this instance, caring for a brood fathered by another male enabled the male to obtain a mate and to father a brood that season. I report here another case in which a male Black-capped Chickadee "adopted" nestlings that he did not father, and increased his own expected reproductive output.

Observations were made during the ninth year of a population study of color-banded Black-capped Chickadees at the Cedar Creek Natural History Area in northern Anoka County, Minnesota. In early April 1985 one chickadee flock consisted of four males and two females. On 21 April, 1985 a third year male, M1, was paired with a first year female, F1, and a second year male, M2, was unmated. On 25 and 28 April M2 was paired with an unbanded female, F2, that almost certainly had arrived on the study area that week. On 5 May M1 and F1 were together and F1 was soliciting food from him, indicating that she had probably begun laying a clutch. M2 and F2 were also together, and F2 was trapped and color banded. On 25 May I found a nest with six 4-day-old nestlings tended by M2 and F1. M1 was not seen again and almost certainly had died. F2 also was not seen again and probably also had died.

At Cedar Creek, Black-capped Chickadees have an incubation period of 12–13 days, and F1's eggs should have been laid on 2–7 or 3–8 May. Because M2 was not with F1 on 5 May, he could not have fathered at least the first 4 eggs, and probably fathered none of them. M2 fed the nestlings and fledglings and behaved in a manner typical of a male parent. No second brood was attempted. This is the only case of brood adoption in Black-capped Chickadees I have seen in 325 nestings.

*Discussion.*—M2 clearly helped raise M1's offspring. From the available evidence, M2 could conceivably have fathered one or two of the brood. If so, he would be expected to increase his reproductive output by caring for the brood, because survival in chickadee broods at Cedar Creek is apparently lower for broods cared for by only one parent. It is highly unlikely, however, that M2 fathered any of F1's offspring before M1 disappeared. Broods of mixed paternity recently have been reported in some avian species (e.g., Mumme et al., Auk 102:305–312, 1985; Gavin and Bollinger, Auk 102:550–555, 1985). Mixed paternity in Black-capped Chickadee broods at Cedar Creek is probably rare or nonexistent as (1) males accompany their mates during the laying period, (2) many pairs are so isolated that the females would have almost no access to males other than their mates, and (3) I have never witnessed attempted extrapair courtship or copulation.

The most probable situation, based on the available evidence, is that M2 fathered none of the nestlings. M2 could have been "primed" to care for nestlings because he and F2 could conceivably have had a nest with eggs that would have hatched about 24 May. Even if M2 fathered none of F1's nestlings, he still could have increased his expected lifetime reproduction by caring for F1's offspring. Male chickadees at Cedar Creek that fledge broods survive from one breeding season to the next at least as well as males that do not fledge broods (64% of 217 vs 51% of 152). Parental care by males apparently does not entail a survival penalty. By pairing with F1 and caring for her offspring, M2 probably increased his chance of mating with her in future years. Eighty-five percent of the chickadee pairs at Cedar Creek in one year breed together the following year, provided both birds survive. Males that retain the same mate from one breeding season to the next fledge, on average, 1.06 more young than do males that acquire a new first year mate. This is due to the greater clutch size of older females compared to first year females ($\bar{x}$ = 6.66, N = 88 clutches, vs $\bar{x}$ = 6.01, N = 134 clutches), and to decreased predation on broods of older females (24% vs 33%). As in the case reported by Odum, brood adoption by the male I observed may actually have increased his expected lifetime reproduction.—James L. Howitz, *Dept. Biology, Univ. Wisconsin–La Crosse, La Crosse, Wisconsin 54601.* *Received 17 Aug. 1985, accepted 2 Nov. 1985.*

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**Brown Thrashers respond to calls of Northern Mockingbird nestlings.**—Adult birds occasionally mistakenly direct attention to young of other species. Most often, this situation occurs when an adult feeds nestlings of another species (reviewed in Shy 1982). An alternative situation occurs when adults become confused and respond to distress calls (e.g., Norris and Stamm 1965) of juvenile birds of a different species. Stefanski and Falls (1972) showed experimentally that adults react to distress calls of juveniles of closely related species. Here I report a field observation of adults responding to distress calls of nestlings of a closely related species.

To capture adult Northern Mockingbirds (*Mimus polyglottos*) on the University of Arkansas, Fayetteville, campus, I place 5–7-day-old nestlings in a circular bal-chatri trap. Females usually land on the trap and "wing-flash" (e.g., Hailman 1960) while looking down at the noisy nestlings, and become tangled in the monofilament nooses on the outside of

the trap. Males, however, rarely approach the trap, and only observe nestlings from some distance.

On 25 June 1983, I color banded three 5–7-day-old mockingbird nestlings (weights = 34.5–35.5 g) and placed them in a trap beneath the nest shrub. Within seconds, a pair of Brown Thrashers (*Toxostoma rufum*) that had been foraging together about 20–30 m from the trap, and whose breeding status I did not know, flew to the noisy nestlings. One bird of unknown sex stood at the side of the trap and began wing-flashing while facing the nestlings inside. The other approached to about 3 m. After about 30 sec, the adult mockingbirds arrived near the trap and drove off the thrashers. The female mockingbird hopped on the trap and wing-flashed, entangling herself in the nooses.

Brown Thrashers are noted for their vigorous defense of nestlings that are giving distress calls (Bent 1948). Brown Thrashers and Northern Mockingbirds are closely related taxonomically (Sibley and Ahlquist 1984), so it seems reasonable to assume that nestling distress calls of these two species are similar, although, to my knowledge, this remains untested. Similarities in nestling distress calls between the two species would explain why the thrashers responded so quickly. I have not observed any other instances of other species responding to mockingbird nestling distress calls.

The calls of mockingbird nestlings elicited behavior in the thrashers similar to those of the adult mockingbirds, confirming that nestling distress calls are capable of stimulating stereotypic behavior patterns in closely related species (Stefanski and Falls 1972). Particularly intriguing is the wing-flashing behavior of the thrasher. Brown Thrashers have rarely been reported to wing-flash (Hailman 1960), whereas mockingbirds wing-flash in a variety of different situations (e.g., Sutton 1946, Hailman 1960, Selander and Hunter 1960, Taylor 1976).

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Kimberly G. Smith, *Dept. Zoology, Univ. Arkansas, Fayetteville, Arkansas 72701.* *Received 13 June 1985, accepted 30 Aug. 1985.*

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**Behavior of a polygynous yearling Yellow Warbler.**—Mating system theory predicts that a female should choose to mate with an already mated male over an available unmated male when the genetic or territorial benefits exceed the cost of decreased male parental care (Searcy 1982). Recently, much attention has been directed at determining what male and territory qualities influence a female bird's decision to mate polygynously (Searcy 1982). Here we report a bigamous mating involving a yearling male Yellow Warbler (*Dendroica petechia*), a primarily monogamous, facultatively polygynous species (Ford 1983). We compared the breeding behavior of this bigamous male with other monogamous males in the population. We examined four measures that have been suggested as potentially important in female choice of a mate: song repertoire size (Krebs 1977), song rate (Greig-Smith 1982), nest defense, and feeding of nestlings.

Observations were made in 1983 on the forested dune ridge near Delta Marsh, Manitoba, in a dense nesting population of Yellow Warblers (Goossen and Sealy 1982). All individuals in the polygynous association were banded: the male (M1) was color banded as a free-flying fledgling the previous year, Female 1 (F1) was color banded as an adult in 1982 (thus was at least 2 years old), and Female 2 (F2) was also banded as an adult in 1982 or earlier. The territory of M1 was situated on the south side of the ridge, which is typically settled first by the earlier-arriving older males (unpubl. data).

F1 was seen regularly (beginning 29 May) in the area of M1's territory several days before M1 occupied the territory. At that time, the area was defended by another yearling male. M1 established himself on the territory on 1 June, apparently in the short interval when the previous owner was removed for individual marking. F1 subsequently remained in the area. A female banded on the left leg with an aluminum band (probably F2, as most females were color marked or not banded at all) was gathering nesting material in M1's territory on 9 June.

The nests of the two females were about 20 m apart. Both contained an egg on 14 June and both had completed clutches of five eggs. On 17 June, M1 moved frequently between the two nests and appeared to courtship feed both females consecutively. F2's nest was destroyed on 23 June on about the sixth day of incubation; F2 was not seen thereafter. F1 successfully hatched all five eggs beginning 27 June, but the nest was empty by 3 July, presumably the result of predation.

*Singing behavior.*—We compared the size of M1's repertoire with those of 10 other individually marked males whose ages were known. Recordings were made between 05:30 and 10:00 from 12 to 20 June using a Dan Gibson parabolic microphone and a Uher 4000 Report-L tape recorder. The average number of songs recorded for each of 11 males was 68 ± 31 [SD]. Song types were analyzed using a Kay Electronics Digital Sonograph 7800 with a medium band setting. A repertoire was considered complete when 20 songs sung produced only two new song types (a very distinct plateau in song types).

M1's repertoire of six song types was the smallest of the repertoires observed ($\bar{x}$ = 8.1 ± 2.0), a trait shared by two other males. Age did not appear to influence repertoire size: the five 2-year-old males sampled had repertoires ranging from the smallest (6 song types) to the largest (12 song types) repertoires recorded.

Song-rate data were collected for M1 and 11 other individually marked males on 3, 6, 7, and 9 June. This was a critical period for mate attraction (first clutch initiation in the population was on 9 June). Song rates were the number of spontaneous songs sung by a male per 5-min sample. We recorded an average of 6 samples (range = 3–7) per bird per day. Song-rate data were collected between 06:00 and 11:00. We collected samples each

hour for each bird. Time of day did not consistently affect song rate due to greater differences in song rates between birds than between hours. On each of the four days sampled, M1 had one of the lowest song rates observed.

*Nest defense.*—We quantified nest defense behavior of M1 and other male Yellow Warblers by examining their response to a human intruder at the nest for a 2-min period. We noted whether the male responded (was seen near the nest), and, if so, his estimated nearest approach. Nest visits occurred usually every second day.

Two visits were made to F2's nest before it was destroyed. On the day before the first egg was laid, M1 responded by coming to within about 5 m of the nest and chipping, but six days later he did not respond. Eight visits were made to F1's nest from Day 3 until Day 18 of the nesting cycle, and M1 responded on Days 8, 10, 14, 16, and 18 with vigorous chipping. His mean nearest approach on these days was 4.8 m. M1's frequency of response and nearest approach were similar to those of other males in the population tested during the same part of the nesting cycle (other males: $\bar{x}$ frequency of response = 57 ± 34.5%, N = 30; nearest approach: $\bar{x}$ = 6.6 ± 2.4 m, N = 29).

*Feeding nestlings.*—We watched F1's nest for a half hour on 1 July and for 1 h on 2 July. A blind was set up 10 m from the nest at least 1.5 h before the nest watches. Observations did not begin until at least 18 min after the observer was settled in the blind. M1 hesitated near the nest, and frequently chipped, despite the precautions we took to minimize disturbances during watches. M1 fed his nestlings only once while F1 made 7, 4 and 1 feeding visits, respectively, during the two nest watches. M1's feeding rate was much lower than the average male feeding rate (3.1 and 4.2 trips/half hour for 2- and 8-day-old nestlings, respectively [Biermann and Sealy 1982]).

*Discussion.*—Although M1 did not fledge offspring in 1983, he did establish pairbonds with more females than did most males in the population. M1 was an unlikely candidate for polygyny, based on several criteria of male quality. First, he was a yearling, and polygyny is usually observed in older males (Weatherhead 1984). Even monogamous older males often have better reproductive success than yearlings (Harvey et al. 1979, Ross 1980). In the case of M1, it is unclear what characters he possessed to merit this success. His advertising behavior and feeding of nestlings were less than those of the average male in the population.

M1's females, however, may have chosen his territory rather than his qualities. This idea is supported by the observation that F1 was seen regularly in the area several days before M1 took ownership of the territory. M1's territory was located on the south side of the ridge, which is settled first by older males (unpubl. data). Females choosing such an area may expect a good territory and a high-quality (older) male. Yet in the following year, M1 returned to this same territory, but attracted only a yearling female. This female fledged two young from a nest in the same tree crotch as F1's nest. Alternatively, F1 may have chosen the previous owner of M1's territory, and then was constrained from sampling other males again when M1 took ownership. Finally, the two females may simply have exhibited suboptimal mate choice.

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MARY L. REID AND SPENCER G. SEALY, *Dept. Zoology, Univ. Manitoba, Winnipeg, Manitoba R3T 2N2, Canada.* (Present address of MLR: *Dept. Biology, Carleton Univ., Ottawa, Ontario K1S 5B6, Canada.*)

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**Range extension of Cayenne Terns on the Puerto Rico Bank.**—The range of the Cayenne Tern (*Sterna sandvicensis eurygnatha*) is described as Aruba, Netherlands Antilles, to Trinidad in the southeastern Caribbean and the Atlantic coast of South America to Argentina (ffrench 1976, Voous 1983). Buckley and Buckley (1984) and Halewyn (1985) have recently discussed the taxonomic problems of its association with Sandwich Terns (*S. s. acuflavida*) in the Caribbean region and elsewhere.

Kepler and Kepler (1978) surveyed Culebra and its adjacent islands, 37 km east of Puerto Rico, for nesting sea birds in 1971. Having discovered colonies, they closely observed >100 of the 735 pairs of Sandwich Terns at cayos Lobito and Matojo for morphological features that would indicate introgression of the Cayenne Tern. They saw no birds having any amount of mottled black and yellow or all yellow bills typical of *eurygnatha.* Norton (1984) reported nesting groups of *S. s. acuflavida* in the northern Virgin Islands, 40 km east of Culebra, with the first mixed pairs of *acuflavida,* the northern form, and *eurygnatha,* the southern form, in the West Indies in 1982. Schaffner and Taylor have conducted seabird studies at Culebra since 1983 and have found no evidence of Cayenne Terns.

On 12 June 1984, Schaffner and Taylor visited Cayo Matojo and counted at least 123 active nests of Sandwich Terns, 103 nests of Royal Terns (*S. maxima*), and 88 nest scrapes perhaps half of which were also *sandvicensis.* Schaffner observed several *sandvicensis* at this colony that exhibited varying amounts of yellow on their otherwise black bills. He also

noticed one incubating individual of pure *eurygnatha* bill color. It appeared that at least 5% of the Cayo Matojo colony had intermediate bills characteristic of birds observed in the American and British Virgin Islands (Norton 1984). Norton and Taylor returned to the colony on 21 June to examine further the *S. sandvicensis* population for evidence of introgression and assortative mating, and to quantify the extent of each as suggested by Buckley and Buckley (1984); but they discovered that the colony had been egged. In any case, the observations suggest that a range expansion occurred within the last few years.

On 30 May 1983, Buckley and Buckley (1984) saw a Cayenne Tern in courtship color at Cape Hatteras Point, North Carolina, within 30 km of two large *S. s. acuflavida* colonies. As suggested by Norton (1984), *S. s. eurygnatha* individuals in the Virgin Islands may have been influenced to return north with overwintering *acuflavida*. Buckley and Buckley (1984) suggest a similar scenario for the occurrence of the first continental North American individual.

The apparent range expansion, notwithstanding greater observer awareness, of the southern form of Sandwich Tern (=Cayenne Tern) to the West Indies in the early 1980s appears to be occurring throughout the local area. We suggest it will continue northward in the Greater Antilles, the Bahamas, and southern North America, where large colonies of *S. s. acuflavida* are found.

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**Downy Woodpecker feeds on insects in a spider's web.**—The taking of prey from spider webs is a rarely reported form of interspecific prey theft. Recent reviews of this phenomenon (Waide and Hailman, Wilson Bull. 89:345, 1977; Brockmann and Barnard, Anim. Behav. 27:487–514, 1979) have documented its occurrence in six avian families: Vireonidae, Trochilidae, Emberizidae, Troglodytidae, Fringillidae, and Bombycillidae. I report this behavior for the Picidae.

On 26 April 1982 at 15:31 (CDT) in the Thunderbird Recreation Area in Walworth County, Wisconsin, I observed a male Downy Woodpecker (*Picoides pubescens*) perched on one branch of a fork atop a ca 10-m snag. Observations were made from the base of the tree with 7 × 35 binoculars. Suspended across the fork was the spider's orb-web that contained numerous small winged insects (ca 2 mm in length). No spider was seen. The woodpecker plucked from the web and ate at least eight of the insects. It then tore down the rest of the web and disappeared behind the branch. It reappeared several seconds later with strands of the web still hanging from its bill and flew from sight. Prior to tearing the web down, the bird did not appear to be entangled in the web, nor did it appear to have webbing in its bill.

Brockmann and Barnard (1979) suggested that collecting of spider webs for nesting material by trochilids may have led birds to stealing prey from webs. Unlike the six families previously reported as feeding on prey in spider webs, *P. pubescens* is not known to collect webs or fibrous material for its nest (Bent, U.S. Natl. Mus. Bull. 174, 1939; Harrison, A Field Guide to Birds' Nests, Houghton Mifflin, Boston, Massachusetts, 1975). Thus, there is no link between web-gathering for nesting material and web-feeding in this species, and why the woodpecker tore down the web remains unknown.

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**Nest-building behavior in a young American Robin.**—On 21 June 1985, in Lawrence, Kansas, I saw a young American Robin (*Turdus migratorius*) at a robin's nest, unused since it was depredated after egg laying in early May. The robin was in fresh juvenal plumage, with a heavily spotted breast and wing coverts; its tail was about full length. The robin crouched in the nest with wings and tail drooping and body feathers fluffed out, and pushed its breast against the nest rim, while kicking backward with its feet. The bird stood up repeatedly and repositioned itself in the nest. These movements closely resembled those used by adults for cup formation and lining the inside of the nest with mud. The bird also stood several times on a branch near the nest edge, pulling at strands of nest material and making tucking movements with them without dislodging any. There was a striking similarity between the movements made by this bird and those of an unmarked adult female building a nest that I had watched several times about 6 weeks earlier. The young robin made nest-building movements at the nest for approximately 15 min. No activity was seen near the nest from 21 June until the nest's destruction in late August.

This appears to be the first record of nest-building behavior in young robins. Hand-reared

young Mistle Thrushes (*T. viscivorus*) showed abortive nest-building behavior in an aviary (Goodwin, Br. Birds 47:81–83, 1953), and a captive 17-day-old Swainson's Thrush (*Catharus ustulatus*) made nest-building movements when held in cupped hands (Dilger, Wilson Bull. 68:157–158, 1956). All three observations of nest-building behavior in young thrushes occurred when the stimulus of an object of appropriate form was present. Juvenile robins have been reported to show other adult reproductive behavior including incubation (D'Agostino et al., Condor 84:342, 1982) and feeding nestlings (Favell, *in* Nice, Trans. Linn. Soc. N.Y. 6:79, 1943).

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**The hiss-display of nestling Black-capped Chickadees in captivity.**—Hissing occurs in many hole-nesting birds (Sibley, Wilson Bull. 67:128–132, 1955), but it is especially prevalent in parids (Hinde, Behav. Suppl. II, 1952). Gompertz (Vogelwelt 88:165–169, 1967) observed the "hiss-display" of a captive adult female Great Tit (*Parus major*) in a nest box. Adult female Black-capped Chickadees (*P. atricapillus*) hissed while being held in a swaying sock (Ficken et al., Auk 95:34–48, 1978) and while in a wire mesh trap (Dixon, Wilson Bull. 95:313–314, 1983). Nocturnal hissing has been reported in nestling Blue Tits (*P. caeruleus*) and Coal Tits (*P. ater*) (Winkel, Vogelwelt 93:68–71, 1972). Nestling chickadees begin hissing at about 12 days of age (Odum, Auk 58:518–535, 1941; pers. obs.). Here we describe hissing by nestling Black-capped Chickadees in the context of nest defense.

From 1979 to 1981 we hand raised four broods of chickadees taken from nest cavities in southeastern Wisconsin. The young hissed on numerous occasions when the cloths covering their bowl "nests" were lifted, and once when one brood was being transported in a swaying mosquito-net hat. Hissing also occurred when one nestling jostled another, sometimes during the night.

Hisses were recorded both in the field and in captivity with a Uher 4200 Report Stereo tape recorder and an Electro-Voice Soundspot 644 or Sennheiser MKH 104 microphone; the calls were analyzed on a Kay 7800 Digital Sona-Graph. The call resembles white noise extending from about 0.5 to 6.0 kHz or more. The mean duration of the hiss in nestlings both in captivity and in natural cavities was 0.90 sec (N = 44, range = 0.30–1.32 ± 0.24 [SD]); this was more than 5 times longer than that reported for adult chickadees ($\bar{x}$ = 0.159 ± 0.072 sec [Ficken et al., 1978]; and $\bar{x}$ = 0.16 ± 0.02 sec, N = 3 [pers. obs.]).

Gradations in intensity were evident in the hiss-displays of the captive nestling chickadees. For example, a nestling sometimes hissed and lunged forward with wings spread, often jumping out of the nest. In other cases, the hiss was accompanied by the wings being spread very quickly in an arc-like fashion forward and downward, with the tail spread and crest raised. This pattern, like that described by Pickens (Auk 45:302–304, 1928), Löhrl (J. Ornithol. 105:153–181, 1964), and Gompertz (1967), often ended with the bird in a posture with the head tucked down and tail up. Hisses were also heard in the absence of any apparent wing-spreading or lunging. On those occasions, the bird hissed and cowered, with its head tucked down and tail up. Nestlings also cowered silently and sometimes hissed without any discernible visual display. These variations in the hiss-display may have been due to one

or more of the following: (1) variable stimulus intensity, (2) the caller's position in the nest inhibiting movement and obstructing our observation, and (3) individual variation.

The behavior of the captive nestlings described here and of adult chickadees reported by Ficken et al. (1978) and Dixon (1983) parallels that of free-living birds in nest cavities. In all instances, the chickadees hissed when disturbed while entrapped in a confined space from which their escape was thwarted. In such a context, the survival value of the hiss probably lies in its ability to startle and deter a potential predator.

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**Nestling Great Crested Flycatcher parasitized by larval fly (*Protocalliphora hirudo*).**—Nestling birds often are parasitized by blow fly larvae (*Protocalliphora* spp.) (Diptera: Calliphoridae), hematophagous parasites that attack nestlings of many nidicolous birds (Gold and Dahlsten, Wilson Bull. 95:560–572, 1983). To the best of our knowledge, this note reports the first known occurrence of *P. hirudo* in the Great Crested Flycatcher (*Myiarchus crinitus*).

On 8 July 1984, we found a nestling Great Crested Flycatcher on the ground at 1080 m in Giles County, Virginia, in an Appalachian mixed-oak forest. The nestling, which was near fledging, had 5 larvae imbedded subcutaneously. Four larvae were located about the head and one larva was in the right wing wrist joint. The larvae were collected, reared to adulthood and identified.

*P. hirudo* apparently is the only Nearctic species in the genus whose larvae are obligate subcutaneous parasites (Bedard and McNeil, Can. Entomol. 111:111–112, 1979). All other *Protocalliphora* are intermittent ectoparasites that live in the nest material (Gold and Dahlsten 1983).

Gold and Dahlsten (1983) reported a single *P. hirudo* larva in the cavity-nesting Mountain Chickadee (*Parus gambeli*). The other North American records for birds infested by *P. hirudo* are for open-cup nesters, probably due to the ease with which ornithologists can find these nests and examine nestlings. Species recorded include: Savannah Sparrows (*Passerculus sandwichensis,* Bedard and McNeil 1979), Wilson's Warblers (*Wilsonia pusilla,* Rausch, Aquilo Ser. Zool. 13:1–4, 1974), Chipping (*Spizella passerina*) and Vesper sparrows (*Pooecetes gramineus,* Bennett, Ph.D. diss., Univ. Toronto, Toronto, Ontario, Canada, 1957), Goldfinches (*Carduelis* spp.), and Yellow Warblers (*Dendroica petechia,* Hicks, Iowa State J. Sci. 46:123–338, 1971).

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# ORNITHOLOGICAL LITERATURE

A Dictionary of Birds. By Bruce Campbell and Elizabeth Lack (eds.). T. and A. D. Poyser Ltd. (England) and Buteo Books, Vermillion, South Dakota (U.S.), 1985:xxx + 670 pp., more than 500 black-and-white photos and drawings. $75.00—This dictionary (encyclopedia would be a better name) boasts a long and honorable ancestry. Alfred Newton published the original version under this title in 1896 and, in 1964, as part of its Centennial observances the B.O.U. published "A New Dictionary of Birds" edited by Sir Landsborough Thomson. This second generation version has long been out of print, so now the B.O.U. has come forth with the third generation. The format is larger than the 1964 version but there are fewer pages. I would judge, however, that the amount of information in this version is greater. One does, however, immediately note the absence of the colorplates that graced Sir Landsborough's dictionary.

From "abdomen" to "zygomatic arch," the coverage is exhausting. No reviewer can claim to have read it all, but the amount of material is staggering. A total of 283 contributing authors are listed together with a long list of people whose entries in the 1964 version have been used with little change. Eighteen artists and 44 photographers are listed. These contributors come from many countries and six continents. Thus, the parochial British emphasis of the earlier edition is somewhat alleviated. Where British and American names of birds differ, care is taken to give each, and, for the most part, the tendency for the British to talk about THE Wren, THE Heron, etc. is avoided.

One of the things that most reviewers of the 1964 edition commented on was the classification used, so we might consider the one used here. The system, which can fairly be described as eclectic, was developed by K. H. Voous, based on his earlier publication of a list of Holarctic birds. Diehard American systematists will rejoice that the nine-primaried assemblage is back in the apparently prestigious final position. Voous recognizes 185 families, giving that rank to taxa that others would rank as sub-families. He points out that avian systematics is in a state of ferment and that it is too early to fully evaluate the many new proposals. The classification in the 1983 A.O.U. Check-list appeared too late to be considered. However, in the entry "DNA and Proteins as Sources of Taxonomic Data" C. G. Sibley presents for the first time in one place the classification of the Passeriformes proposed by him and J. A. Alquist.

Each family is discussed in an entry by a well-known expert in that group, entered according to the English name, but is cross-indexed by the scientific name. The amount of detail varies with the size of the family. Small families probably have each species mentioned, but the larger ones have only a few. The discussions include, usually, such topics as Characteristics, Habitat, Movements, Food, Behavior (oops—Behaviour), Voice, and Breeding. I found these authoritative and informative for those groups with which I am most familiar. A line drawing of one species of each family is included.

In addition to the discussions of the families, there are essays of varying length on a variety of topics: e.g., 4¾ pp. on Flight, nearly 5 pp. on Biostatistics, 4¼ pp. on Migration. It is difficult to think of a topic related to birds that is not included. The ones that I have read carefully seem relatively error-free. The general level is rather high, and only the real experts in a given area will find the accounts superficial.

Now and then British parochialism does creep in. The article on Census implies that between 1944, when Williams published his spot-map method, and 1959 little use was made of this technique, which was finally given the "seal of approval" by the B.T.O. in 1962–64. This certainly overlooks the dedicated corps of contributors to the Breeding Bird Census

published by American Birds and its predecessor, Audubon Field Notes, through all these years. This entry also makes no mention of the Breeding Bird Survey method which has given such interesting results in this country, nor of the "variable circular plot" method so widely used by census takers in North America.

With so many authors expressing so many points of view, the editorial task of assuring internal consistency must have been monumental. In general it seems to have been done outstandingly well. I noted only one slip. The author of the entry on the Dodo (*Raphus cucullatus*) rejects Storer's proposal that there are two families of didine birds, while Voous' classification does recognize this.

In summary, this is a job well done. The price is steep, but the information is invaluable. Even the seasoned professional would be wise to read the appropriate entry when starting a new line of research.—GEORGE A. HALL.

PRIMER SYMPOSIO DE ORNITOLOGIA NEOTROPICAL (14–15 OCTUBRE 1983, AREQUIPA, PERU). By F. Gary Stiles and Pedro G. Aguilar F. (eds.). Asociación Peruana para Conservación de la Naturaleza, Lima, 1985:126 pp., 43 figs., 10 half-tones, 25 tables. $6.00 (paper). Available from: APECO, José Quiñones 226, Lima 18, Peru (checks in U.S. dollars accepted).—In his capacity as President of the IX Congreso Latinoamericano de Zoología, held in Arequipa, Peru, in 1983, the junior editor conceived the idea of convening a symposium on Neotropical ornithology to be held in conjunction with the larger Congress. With the support of Susana Moller-Hergt, President of APECO, the symposium was organized by Peruvian ornithologists Manuel Plenge and Humberto Tovar. Thirteen of the contributed papers are published in full in the present volume, and 19 more are published in summary form. The 43 authors are from Peru (13), the United States (8), Spain (5), Chile (4), Argentina, Bolivia, Mexico, and Paraguay (2 each), and Costa Rica, Cuba, Ecuador, and Venezuela (1 each).

All of the papers are in Spanish; those that are published in full have English abstracts, which vary in their comprehensiveness. A few of the major papers are general summaries: O'Neill on avian distribution in Peru, Wiley on the U.S.F.W.S. Endangered Species Program (highlighting the Puerto Rican Parrot [*Amazona vittata*]), and Freese on international cooperation in the conservation of migratory birds in the Western Hemisphere. The remaining papers present original data. Of these, four deal with avifaunas: Escobar and Salomon on the university campus of San Lorenzo, Paraguay; Munn on Manu National Park, Peru; Nocedal on the Valley of Mexico; and Stiles on altitudinal distribution of the birds of the Caribbean slope of central Costa Rica. Six treat some aspect of the biology of single species: Castro on altitudinal adaptations in *Zonotrichia capensis*; Guerra C. and Cikutovic S. on reproduction of *Pelecanus occidentalis thagus*; Bellocq and Kravetz on rodent predation by *Athene cunicularia*; Hays on distribution and abundance of *Spheniscus humboldti*; Wallace, Temple, and Torres A. on the ecology of *Vultur gryphus*; and Cikutivic S. and Guerra C. on the ecology of *Larus pipixcan* on its winter range in Chile.

Unlike many more expensive symposium proceedings, this volume was *not* printed from nonjustified typescript. Reproduction of the photographs is relatively coarse, and some readers may find the typeface of the figure captions (especially when lengthy) uncomfortably small. Otherwise the appearance of the pages is as attractive as that in most international journals.

Although the contents are somewhat heterogeneous, the modest price of this publication should permit its addition to the libraries of all students of neotropical birds. Some of the papers, such as those on the Andean Condor and Humboldt Penguin, will be important to

the evaluation of conservation measures for these species, and others represent good original contributions to life history information on species well studied in North America but much less so in South America, such as the Brown Pelican and Burrowing Owl.—KENNETH C. PARKES.

THE FLORIDA SCRUB JAY: DEMOGRAPHY OF A COOPERATIVE BREEDING BIRD. By Glen E. Woolfenden and John W. Fitzpatrick. Princeton Univ. Press, Princeton, New Jersey, 1984: 406 pp., 88 numbered text figs. (including 10 black-and-white photos) plus 12 maps and figures in the appendixes, 60 tables. $45.00 (cloth), $14.50 (paper).—My perspective in reviewing the "The Florida Scrub Jay" is not that of an individual actively involved in social-system research, and in particular not that of someone with a stake in the resolution of major questions concerning the evolution of cooperative breeding systems. Instead, my interests come from general concern with current issues in behavioral ecology and the ongoing desire to bring to classroom lectures information which both stimulates attention and focuses on these issues. To others with similar intents, I can only say that Woolfenden and Fitzpatrick's monograph serves these purposes superbly.

Florida Scrub Jays (*Aphelocoma c. coerulescens*) are year-round residents in oak scrub community in central Florida. All suitable habitat is occupied by jays, divided into vigorously defended territories; thus, the habitat is "saturated." Although the fundamental social unit is the mated pair, nonbreeding helper jays live on almost half the territories. These auxiliary birds are often, but not always, offspring of one or more previous breeding efforts by the resident pair. They "help" defend the territory and feed nestlings and juveniles, but they disperse to become breeders whenever the opportunity arises. Sometimes, a male helper will replace an ailing or dead male breeder on his own territory.

Glen Woolfenden began studying Florida Scrub Jays in 1969 at the Archbold Biological Station. He was joined soon after by John Fitzpatrick, then an undergraduate. By 1979, together they had color banded a total of 725 jays in their study area, gathered detailed data through time for about 30 mapped jay territories, and published a series of papers addressing various aspects of the jay social system. By the decade mark, Woolfenden and Fitzpatrick had obtained a wealth of demographic information, summarized thoroughly and thoughtfully in "The Florida Scrub Jay." In the preface they point out that first authorship was "determined by a coin toss."

Each chapter in the book is a concise package, usually with an introductory synopsis and final section of specific conclusions. Tables display all data discussed, and figures are effectively used to show relationships among variables or illustrate hypotheses. The appendixes are extremely useful for following text narrative, including a vegetation map of the study area and 10 years of maps of Scrub Jay territories, which clarify a number of the case histories discussed. Ten chapters present the relevant data and final synthesis: Introduction (which states objectives and organization of the book), Procedures, The Scrub Jay in Florida (which discusses the historical origins of the Florida Scrub Jay population and the vegetational composition of the habitat), The Pair Bond, Helpers, Territory, Dispersal, Reproduction, Survivorship and the Life Table, and Evolution of Florida Scrub Jay Sociality.

The latter two chapters present an excellent synthesis of the data presented in earlier chapters. Survivorship and the Life Table (chapter 9) summarizes the demographics of the Florida Scrub Jay, presenting survivorship and $l_x m_x$ curves, age structure diagrams, and life tables (particularly Table 9.7). Important facts to emerge from this discussion include a stable age structure, high juvenile mortality with great annual variation, relatively higher breeder survivorship (0.820 annually for both sexes), low female helper survivorship, and

high survivorship for those helper males that do not leave their natal territory. An additional point of interest is that breeders with helpers have a significantly lower annual death rate (15.3%) than breeders without (23.2%). Woolfenden and Fitzpatrick discuss how closely the demography of their jay population resembles the classic (but controversial) K-strategy; in addition, the life history traits characterizing the jay population are predicted from two different life history models—adaptation to a stable, saturated environment and to highly variable juvenile mortality.

Chapter 10 examines the demographics of the Florida Scrub Jay in relation to the evolution of cooperative breeding. The major issue is whether kin selection (i.e., "indirect" selection component) in addition to individual selection (i.e., "direct" selection component) has played a role in the evolution of this cooperative breeding system. Algebraic and graphical models nail down the critical variables (summarized in Table 10.1) involved in elucidating this question, and the 10-year data sets provide some interesting answers. The models should be applicable to other studies of cooperative breeding; the results will be of great interest to all workers in the field. In addition, previous use of per capita fitness estimates is criticized by Woolfenden and Fitzpatrick. The case is made for an approach based on lifetime reproductive success of alternative reproductive strategies (which has been used for some time by the "life history traits" people). The models of Woolfenden and Fitzpatrick show in increasing complexity the conditions favoring delayed dispersal, with and without the added kinship component. Basically, as juvenile survivorship increases on the parental territory, jays gain more by staying home and helping. Next, the kinship coefficient (k/R) is devised to measure the relative contribution of any kinship effects on fitness. Woolfenden and Fitzpatrick conclude that a nondispersal strategy with helping behavior can arise in either the presence or absence of kin selection, depending on survivorship, probability of successful dispersal, and annual probability of a surviving helper becoming a breeder. Adding some kinship does ease the conditions favoring delayed dispersal. By plotting the values for Florida Scrub Jay life history traits on their graphical models, Woolfenden and Fitzpatrick discover that males plot out within the area where delayed dispersal and helping behavior are favored (without a kinship component), whereas females do not. This agrees with observations of sexual differences in dispersal strategies. Woolfenden and Fitzpatrick conclude (p. 339) that "The system appears to be strongly favored by direct, cost-benefit relationships regarding breeding space competition, quite independent of the addition of a kinship component to inclusive fitness." A discussion follows comparing social systems among the *Aphelocoma* jays, constructing a model for the evolution of cooperative breeding. The western Scrub Jays and "Mexican Jays" (*A. ultramarina*) are considered extremes on the social continuum, with the Florida Scrub Jay one step removed from the multipair territorial system of the Mexican Jay.

One of the best features of "The Florida Scrub Jay" is its clear, simple writing style. Great care has gone into each statement of fact, statistical result, hypothesis, and conclusion. My minor criticisms of the book, given here only for completeness, must not deter the reader. Information in Stallcup and Woolfenden (1978) on feeding rates and implications would be helpful in chapter 5. The discussion of why helpers help seems important enough to merit an earlier and better developed treatment than given in chapter 10. I found only two typos and use of "quantitative" when "qualitative" was meant. Also, Table 5.2 displays raw data and not true "ratios."

Glen Woolfenden and John Fitzpatrick have recently completed their seventeenth consecutive field season (!) of work on their population of jays. From their studies, the value of long-term data is extremely clear. Only with such data can the life history strategies of a population be characterized and ultimate questions concerning the evolution of helping behavior and delayed breeding be tackled. For its valuable data, synthesis, and pertinence

to all studies of social systems, "The Florida Scrub Jay" is an important achievement. For Woolfenden and Fitzpatrick, future direction has emerged from past findings: efforts are now focused on answering questions pertaining to what resources are limited, "the relationships between habitat quality, prey density, and territory size," and "the effects of seasonality," (i.e., fundamental driving forces of this cooperative breeding system). Surely, the wonderful rewards from long labor should make an impression on even the most impenetrable students in our ecology and behavior courses.—DIANA F. TOMBACK.

THE PUFFIN. By M. P. Harris. Illustrated by Keith Brockie. T. and A. D. Poyser Ltd. (England) and Buteo Books, Vermillion, South Dakota, 1984:224pp., 24 black-and-white plates with caption figs., 47 numbered text figs. $32.50.—Since the publishing of Ronald Lockley's book, "Puffins," in 1953, much has been learned about the Atlantic Puffin (*Fratercula arctica*), the subject of both Lockley's earlier work and this important new title by Michael Harris. Harris has successfully reviewed the puffin literature and included many of his own insights into the life of this puffin. "The Puffin" is written for a broad audience that includes both serious amateurs and seabird biologists. The text is very readable, yet there is no shortage of detail about puffin biology. Excellent black-and-white photographs illustrate subjects as diverse as puffin habitats to Faroe Islanders draped with a day's catch of several dozen puffins. The book also contains 47 maps and graphs showing the distribution of colonies and many aspects of puffin growth and development.

Most North American readers will not be interested in the details of puffin distribution in Britain and Ireland, but this is balanced by an overview of puffin populations outside Britain and Ireland. The chapters on breeding biology, food and feeding, growth of young, cycles of puffin attendance at colonies, and migration and survival are all rich with Harris' own research and contain much new information as well as reviews of the subjects to date. The chapter titled "Behaviour" (by K. Taylor) will prove very useful to future puffin observers as it provides a working inventory of puffin behaviors, many of which have not previously appeared in the puffin literature.

The chapters titled "Predators, Pirates and Competitors," "Man and Puffins," and "Pollution" contain information that should interest anyone with a concern for the future of puffins and other seabirds, most of which share similar problems with puffins. "The Puffin" also contains an appendix consisting of twenty tables with detailed information about timing of breeding, body measurements, breeding success, weights of fish loads, and many other details.

My only issue with the book is that after discussing current conservation problems ranging from oil pollution to food shortages, Harris concludes that the "general state of Puffindom is better than at any time this century." This is misleading because this century follows a period of ruthless exploitation to puffin populations on both sides of the Atlantic that was at its worst in the late 1800s. Also, while it is no doubt true that certain areas rich in food such as the Isle of May, where most of Harris' work was done, have shown spectacular recent increases, very little is known about population size and reproductive success for puffins in most of their vast northern range. This is especially true in Iceland where most puffins live.

"The Puffin" is an important addition to the literature about this abundant and appealing bird. I enthusiastically recommend it to any reader interested in detailed life histories and biology of seabirds.—STEPHEN W. KRESS.

MARINE BIRDS: THEIR FEEDING ECOLOGY AND COMMERCIAL FISHERIES RELATIONSHIPS. By D. N. Nettleship, G. A. Sanger, and P. F. Springer (eds.). Special Publication, Canadian Wildlife Service, Ottawa, 1984:220 pp., not indexed. Available at no charge from Distribution Section, Canadian Wildlife Service, Department of the Environment, Ottawa, Ontario, Canada K1A 007.—The 23 papers in this volume were presented as a special symposium at the eighth annual meeting of the Pacific Seabird Group in January 1982. Following the format of the symposium, the book is divided into three parts: I. The feeding ecology of marine waterfowl (6 papers), II. The feeding ecology of pelagic marine birds (7 papers), and III. Seabirds and commercial fisheries interactions (11 papers). Forty-two researchers contributed.

The collected papers present a good, but perhaps rather skewed, compilation of research on the feeding habits of marine birds and their relationships to commercial fisheries. The waterfowl studies include information on diet, seasonal changes in foraging periods and habitats, and food and habitat resource partitioning. The second part includes papers that are quite diverse and develops concepts that will be very useful to students of pelagic birds. Major topics include diet and energy gain, the roles of autumn upwelling, olfactory foraging, feeding rates and diet changes related to nesting, and comparative foraging distribution of various seabirds. The section on commercial fisheries as it relates to seabirds documents both positive and negative effects of modern fisheries on seabird populations. Several chapters provide good overviews of the subject and biological information on prey species.

The individual chapters are both well written and well edited. A numbered system of headings and subheadings with appropriate type faces makes location of specific information easy. Tables and figures are uniformly prepared and articulate (something often overlooked in volumes of this type). Abstracts are presented in both English and French. The 23 chapters are short and vary in length (3–13 pages) and significance.

One handicap of any symposium of this type is the cumulative problem of maintaining uniform coverage from combined contributed papers. This volume suffers geographically in that a tighter area of coverage, in my opinion, would make its usefulness more focused. For example, all the marine waterfowl studies were in the North Pacific (5 of 6 in Alaska), and all but five of the seabird papers discuss the North Pacific (four are for the North Atlantic and one for South Africa). Taxonomically, primary species discussions cover only Anatidae (6), Procellariidae (3), all on Sooty Shearwaters (*Puffinus griseus*), Pelecanidae (1), Phalaropodidae (1), and Alcidae (5). No chapter discussions of major marine bird groups such as penguins, loons, grebes, albatrosses, storm-petrels, jaegers, gulls, or terns are provided, although four chapters present limited information on seabird communities or ecological concepts that include information on some of these groups.

Lack of a formal introduction and a summary of the entire volume or its three sections lessens the volume's ability to achieve any specific focus or to assist the casual reader in appreciating the patterns that accumulate from related chapters.—DAVID S. LEE.

THE MARSH HEN, A NATURAL HISTORY OF THE CLAPPER RAIL OF THE ATLANTIC COAST SALT MARSH. By Brooke Meanley. Tidewater Publishers, Cornell Maritime Press, Centreville, Maryland, 1985:123 pp. $8.95.—For some of us the sight of a marsh brings forth a strange itching among the toes, an almost overpowering urge to plunge in. A colleague jokingly chides that we need to soak our webs. Brooke Meanley is obviously such a biologist—and his plunges, backed by a fine ability to see, understand, and artfully describe, have yielded a quantity of informed research on marsh species.

His most recent publication, "The Marsh Hen" summarizes his years of observations on Atlantic salt-marsh ecology, and particularly his studies of the nesting populations of the Clapper Rail (*Rallus longirostris*); it brings together the most important literature (1808–1983) on those populations. It contains less original research than did his parallel study of the King Rail (*R. elegans*) (North Am. Fauna 69:1969), and is written in a more informal style appropriate for a paperback aimed at both the scientists and the informed layman.

The 12 2–17-page chapters cover the waterfront, from discovery and history, Clapper-King Rail relationships, habitat, feeding behavior, nesting, etc., through natural catastrophes, predators, and pollution. Five appendixes discuss the subspecies found in the United States, sexing and aging, methods of capture and censusing, and scientific names used in the text.

The book is well-illustrated with excellent photographs of salt-marsh life and ecology as well as with superb photographs of Clapper Rails, mostly by the author, and with pleasing to very nice black-and-white drawings by John W. Taylor, who also did the colored cover.

Criticisms are minimal, considering the broad audience for which the book was designed. I was amused at the tertiary references cited for the relationships of the King-Clapper Rail complex (Mayr and Short 1970, Ripley 1977), when Meanley's own work, in a large part, formed the basis for those pontifications. I believe too much credence was placed on Christmas Counts for winter abundance and fluctuations, and I would have predicted the Black-crowned Night-Heron (*Nycticorax nycticorax*) would be on the list of predators. But this is carping. "The Marsh Hen" is a must for all game managers dealing with aquatic birds, and for all those with swamp mud in or on their shoes. It will edify and entertain all who enjoy good field natural history and good writing.—ROBERT W. DICKERMAN.

THE PARASITIC COWBIRDS AND THEIR HOSTS. By Herbert Friedman and Lloyd F. Kiff. Proceedings of the Western Foundation of Vertebrate Zoology, Vol. 2, no. 4, 1985:pp. 227–302. $10.00—This publication summarizes the series of seven papers on parasitic cowbirds begun by Herbert Friedman back in 1929 and adds new records since the last listing was published in 1977. Up-to-date catalogs of the hosts of three parasitic species are presented with detailed subspecific allocations for both hosts and parasite. The listings now include 220 species (389 species and subspecies) parasitized by the Brown-headed Cowbird (*Molothrus ater*), 201 species (264 species and subspecies) parasitized by the Shiny Cowbird (*M. bonariensis*), 77 species (98 species and subspecies) parasitized by the Bronzed Cowbird (*M. aeneus*), and 1 species (*M. badius*) parasitized by the Screaming Cowbird (*M. rufoaxillaris*).

The high rate of egg mortality would seem to make brood parasitism a perilous way of life, but all three cowbird species are doing well and all are expanding their ranges. The authors discuss this matter and conclude that the evidence available points to a very high fecundity in cowbirds. The underlying mechanisms remain unclear, but cowbirds do lay more eggs than do nonparasitic passerines, and the female cowbirds appear to be somewhat released from normal hormonal restraints that restrict the number of developing follicles in the ovary.

The book is a valuable and informative summary of present knowledge.—GEORGE A. HALL.

JOHANN FRIEDRICH VON BRANDT: *ICONES AVIUM ROSSICO-AMERICANARUM. TABULAE VII, INEDITAE*; WITH COMMENTS ON BIRDS, EXPEDITIONS AND PEOPLE INVOLVED. By Bernt Løppenthin. Scandinavian fine Editions, Copenhagen, Denmark, 1984:70 pp., 11 text fig., 1 uncolored and 7 colored plates. 385 DKr.—In 1872, Otto Finsch published a paper in which

he made reference to a set of seven colored lithographs of 49 birds from the north Pacific and adjacent coastal areas (Finsch, Abh. naturw. Ver. Bremen 3:17–86, 1872). These plates were drawn around 1835 by W. Pape for Johann Friedrich von Brandt, presumably to illustrate a major treatise on the birds of Russian America. Brandt's monograph was never completed, however, and the plates remained unpublished. Very few sets apparently were produced, and their existence essentially was forgotten until 1971, when a complete set from a private collection was brought to the library of the University of Copenhagen for identification (the set has since been donated to the Library). The discovery of these plates prompted Bernt Løppenthin, at that time the chief librarian at the Scientific and Medical Department of the University Library, to research the provenance of this material and to review the history of exploration and discovery in the far northern Pacific Ocean and the surrounding coastal areas. These studies uncovered new information of interest to historical ornithology and corrected a number of misunderstandings in the literature. Dr. Løppenthin's results are presented in this book.

A principal motive for the choice of a large format (overall dimensions of 27.5 × 32.0 cm) is the publication of Brandt's plates; these are very nicely reproduced in color with an additional black-and-white copy of Brandt's Plate I showing the handwritten notes (ca 1839) of the Danish zoologist D. F. Eschricht. The text is divided into several sections including a short biography of Brandt, an account of the explorations of the North Pacific up until 1835, and comments on each of the species illustrated in the plates. An extensive list of references and a thorough index complete the volume.

Despite acknowledged assistance with the language, the text reads as though it were written by someone not comfortable with English; many of the grammatical constructions are odd and the style is quite disjointed. It might have been better if the manuscript had been written in Danish and then translated. However, the scholarship is considerable, and Dr. Løppenthin appears to have been quite thorough in reviewing the primary literature (much of which is obscure). The extensive notes dealing with each of the birds illustrated in Brandt's plates analyze the nomenclatural knots surrounding many of these species as well as comment on past and current distributions and the history of discovery of these birds.

At first glance this volume appears to belong with the growing number of books devoted to ornithological illustration. However, it deserves a much wider audience because of the variety of taxonomic, biogeographical, and historical information covered. That this information is sometimes difficult to extract is a relatively minor criticism. Any serious ornithological library should acquire this volume, and students of the birds of the North Pacific should find it quite useful.—D. Scott Wood.

Eskimo Year. Second Edition. By George Miksch Sutton. Univ. Oklahoma Press, Norman, Oklahoma, 1985:321 pp., 48 black-and-white photographs, 24 drawings. $14.95.—George M. Sutton has long been acclaimed not only for his artwork and scientific endeavors but also for his popular writing. His reputation in this latter arena was initiated with the first edition of "Eskimo Year," first published in 1934 and reprinted in 1936, but long out of print and not readily available to recent generations of naturalists. This new edition, differing from the first only by the addition of a new preface by Dr. David F. Parmalee, remedies this situation.

"Eskimo Year" is the story of the year that Sutton spent with the Aivilikmiut (walrus-hunting) Eskimos on Southampton Island in the Canadian Arctic. This part of the world was little known at the time of Sutton's visit (1930), although the trappings of western civilization were becoming an increasingly large part of the Eskimo's life even then. The visit meant a radical change in comfort and life style for Sutton and proved to be an adventure

of the first order. Fortunately for those of us not wishing (or able) to forsake the comforts of home, Sutton has provided a vicarious adventure to the far north.

Sutton was first an artist; all his actions were influenced by artistic considerations. Thus the book, although chronologically arranged, is a series of individual detailed sketches taken from his year's experience. Sutton's pen-and-ink drawings are liberally sprinkled through the text, and his photographs provide further documentation of the people and scenes described. The author's love of the Arctic and its people and wildlife is apparent in each chapter, but he also conveys the awe with which such a harsh environment must be viewed. That the expedition was primarily scientific (the technical results were published as Vol. XII, Part 2, Mem. Carnegie Mus., 1932) is clear from the accounts, but the emphasis here is on the interaction between Sutton and the Eskimos he lived with. The images he projects are important historically because so much has changed for the Eskimos in the past half century. I thoroughly enjoyed the book and recommend it not only to those with an interest in the Arctic but to all who are armchair adventurers.—D. Scott Wood.

The Status and Distribution of New Jersey's Birds. By Charles F. Leck. Rutgers Univ. Press, New Brunswick, New Jersey, 1984:214 pp., 1 map, 2 Tables. $25.00 (cloth).—This 9½″ × 6⅛″ book is written in an easily readable style, has large print, and no illustrations. Its introduction cites the diversity of habitats and birdlife in New Jersey. Included are 450 species, 36 of which "need better confirmation—to consider them fully documented for New Jersey." Nomenclature follows the A.O.U. 6th edition Check-list. With a few species Leck uses two English names; the A.O.U.-chosen name and a second one used widely in recent field guides. The first Table gives additions to New Jersey avifauna, 1960–1981, including 36 species, 8 of which are shown with a "?"—those with some problem of identification, or of origin (wild or escaped). The questioned entries include Yellow-billed Loon (*Gavia adamsii*), Rufous-necked Stint (*Calidris ruficollis*), and Band-tailed Pigeon (*Columba fasciata*), each with some question of accuracy in identification. Table 2 lists 28 species new to the list of breeders within the state, most added since 1920. Included here are Glossy Ibis (*Plegadis falcinellus*), Black Vulture (*Coragyps atratus*), Chuck-will's-widow (*Caprimulgus carolinensis*), and White-throated Sparrow (*Zonotrichia albicollis*).

The main part of the book, Species Accounts (169 pages), gives the English and Latin names for each species, general distribution in this hemisphere, and current status in New Jersey. The latter includes the usual set of classes—migrant and winter resident, breeder, summer resident, etc., with modifiers such as rare, common, abundant, hypothetical, and extinct, etc. Although each species occupies only one or two paragraphs, with two or three species per page, considerable information is given for migratory habits, nesting habitat preferences, and periods of abundance. Specific arrival and departure information is lacking. The principal emphasis in the Species Accounts, and perhaps the only really innovative information in this type of book, is the citing of "high counts" of bird numbers, either single-day counts, season totals, in some cases breeding pair counts, or counts of birds banded in a season or a day. One or more type of count is given for about 250 species, mostly the more common birds, but also for some that are strictly migratory in the state. Examples include: Fall season banding total, Sharp-shinned Hawk (*Accipiter striatus*)—3539, Cape May, 1979; Northern Saw-whet Owl (*Aegolius acadicus*)—110, Cape May, 1981; Yellow-bellied Flycatcher (*Empidonax flaviventris*)—51, Island Beach, 1963; Single-day counts, American Kestrel (*Falco sparverius*)—24,875, Cape May, 15 Oct. 1970; Short-billed Dowitcher (*Limnodromus griseus*)—25,000, Brigantine National Wildlife Refuge, 2 Aug., 1972; Eastern Bluebird (*Sialia sialis*)—750–1000, Cape May, 28 Oct., 1981; and Breeding pairs (in one area), Marsh Wren (*Cistothorus palustris*)—160, Troy Meadows, 1947; Brown

Thrasher (*Toxostoma rufum*)—est. 200, Sandy Hook, June 1976. No citations of published accounts are given for these or other high-count information data.

A major fault in the main body of the text is the inclusion of reliable *and* unreliable information in the Species Account section. The author apparently wrestled with the problems of what to do with single sightings—Brown-crested Flycatcher (*Myiarchus tyrannulus*), a single bird, considered hypothetical, Brown-headed Nuthatch (*Sitta pusilla*), one at a suet feeder in 1876; and Whooping Crane (*Grus americana*), which "at one time probably occurred along the Atlantic coast, including New Jersey, during migration." In addition, several introduced birds which failed to survive have been listed, e.g., Eurasian Skylark (*Alauda arvensis*). All of the above are listed in the main text of the Species Account, along with the reliable known breeding or migrant birds! This adds to the reader's confusion—what is the New Jersey bird list?

Following the Species Account is the section, Unestablished Exotics, Escapes, and Unsuccessful Introductions (8 pp., 38 species), which is seemingly a better place for the entries in the paragraph above.

The next section, A Guide to Lesser Known Locations (4 pp., approximately 120 named locations) is a list of towns, marshes, inlets, reservoirs, etc. cited in the main text as locations where specific birds have been found, counted, or banded. The only map in the book is of New Jersey, with only the county outlines given. It would have been helpful if the list of places had been numbered, and the numbers inserted in a map. Spare pages were available; pages 12 and 182 are completely blank.

A 6-page Bibliography includes recent ornithological references covering New Jersey, and also parts of the neighboring states of Pennsylvania, New York, and Delaware. Finally, a 14-page Index lists all the English and Latin names in the book.

For those interested in the high-count data, and distributional material for birds of the state, the book is recommended, but as a definitive list of birds of New Jersey, I am led to withhold my recommendation.—George B. Reynard.

Hawaii's Birds. 3rd Edition, revised. By Robert J. Shallenberger (ed.). Hawaii Audubon Society, Honolulu, Hawaii, 1984:96 pp., numerous color photographs, paintings, and maps. $4.95 (paper).—This is a revision of the standard field guide and brief introduction to the Hawaiian avifauna, previously reviewed in The Wilson Bulletin (96:152, 1984). Order by mail from the Hawaii Audubon Society, Box 22832, Honolulu, Hawaii 96822. Add $0.70 postage for surface delivery or $1.03 for air mail.—Robert J. Raikow.

## BRIEFLY NOTED

An Annotated Bibliography of Literature on the Spotted Owl. By R. W. Campbell, E. D. Forsman, and B. M. Van Der Raay. Land Management Report No. 24, Ministry of Forests, Province of British Columbia, Victoria (Available from Queen's Printer, Victoria, B.C.), 1984:116 pp., $7.50—Contains 586 entries arranged alphabetically but indexed by subject and geographical area. The annotations average about one sentence each.—G.A.H.

A Natural History of Digges Sound. By A. J. Gaston, D. K. Cairns, R. D. Elliot, and D. G. Noble. Canadian Wildlife Service, Report Series No. 46, 1985:62 pp, many black-and-white photos, maps, and graphs. $8.00 (in Canada), $9.60 (elsewhere).—Despite the

title, this work concentrates on the seabirds: eiders, gulls, one tern, and 4 alcids. Notes on breeding biology are given, and predation by falcons, foxes, and ravens is discussed.—G.A.H.

BIRDS OF THE NASHVILLE AREA. Fourth Edition. By David F. Vogt, C. Gerald Drewry, Paul B. Hamel, and Stephen J. Stedman. Nashville Chapter, Tennessee Ornithological Society, 1985:iv + 60 pp. $4.00 (obtain from the Treasurer, Nashville Chapter, T.O.S., P.O. Box 24573, Nashville, Tennessee 37202-4573)—Lists 306 species known for the region with brief annotations, and the conventional bar graphs showing seasonal occurrences and abundances.—G.A.H.

ILLINOIS BIRDS: VIREOS. By Jean W. Graber, Richard R. Graber, and Ethelyn L. Kirk. Illinois Natural History Survey Biological Notes 124, Champaign, Illinois. 1985:38 pp., 27 black-and-white figs., photographs, graphs and maps. No price given.—This is the tenth in a series of short publications being issued in lieu of a state bird book. Each of the seven species accounts includes sections on Spring Migration, Distribution, Nesting Habitats, and Populations (for the 6 nesting in Illinois), Nesting Cycle, Fall Migration, Food, and Specimen Data. A map of the continental range and one of the Illinois range, a photo of the bird at the nest, a graph showing the egg-laying and migration seasons, and tables of spring and fall densities are included for each species. A valuable and informative publication.—G.A.H.

*Wilson Bull.*, 98(2), 1986, pp. 333–334

# ANNOUNCEMENTS

## SECOND VICE-PRESIDENTS OF THE WILSON ORNITHOLOGICAL SOCIETY

In anticipation of the 100th anniversary of The Wilson Ornithological Society, The Wilson Bulletin is publishing a series of lists compiled by John L. Zimmerman of the past and present officers and Council Members of the Society. Below is a list of the Second Vice-Presidents of The Wilson Ornithological Society.

Josselyn Van Tyne, 1932
Alfred M. Bailey, 1933–1934
Margaret Morse Nice, 1935–1936
Lawrence E. Hicks, 1937
George Miksch Sutton, 1938–1939
S. Charles Kendeigh, 1940–1941
Olin Sewall Pettingill, Jr., 1942–1943
Harrison F. Lewis, 1944–1946
Maurice Brooks, 1947–1948
Walter J. Breckenridge, 1948–1950
Burt L. Monroe, Sr., 1950–1952
Harold F. Mayfield, 1952–1954
Lawrence H. Walkinshaw, 1954–1956
Phillips B. Street, 1956–1960
Roger Tory Peterson, 1960–1962
Aaron M. Bagg, 1962–1964
H. Lewis Batts, Jr., 1964–1966
William W. H. Gunn, 1966–1968
Pershing B. Hofslund, 1968–1969
Kenneth C. Parkes, 1969–1971
Andrew J. Berger, 1971–1973
Douglas A. James, 1973–1975
George A. Hall, 1975–1977
Abbot S. Gaunt, 1977–1979
Jerome A. Jackson, 1979–1981
Clait E. Braun, 1981–1983
Mary H. Clench, 1983–1985
Jon C. Barlow, 1985–

## FIRST GEORGE MIKSCH SUTTON AWARD FOR ORNITHOLOGICAL ART

In June 1985, at the joint meeting of the Wilson and Cooper ornithological societies, a panel of judges selected Karen Lynn Allaben-Confer as the recipient of the George Miksch Sutton Award for Ornithological Art. Her painting, "Razorbills" (*Alca torda*), is the Frontispiece of this issue of *The Wilson Bulletin.*

Karen lives in Brooktondale, New York, near Ithaca. She graduated in 1969 from Ithaca College (B.A. in Biology), where her illustrations of faculty publications, classroom visual aids, Ph.D. theses, and rough sketches for freshman chemistry and biology texts were exchanged for tuition. Her marriage in 1974 to John L. Confer, Associate Professor of Biology at Ithaca College, germinated her ornithological career. In 1976 she traveled to Trinidad to study with noted artist Don Eckelberry.

Karen has organized and exhibited in three major group shows at the Cornell Laboratory of Ornithology. Her first major single-artist exhibition, "Release the falcon—a visual life history of the Peregrine Falcon," was exhibited at Cornell in 1981. She has also exhibited at the "Birds in Art" show at the Leigh Yawkey Woodson Art Museum in Wausaw, Wisconsin, after which her paintings toured the U.S.

Karen was Art Editor for *New York Birders,* the newsletter of the Federation of NYS Bird Clubs, and has published in *American Birds, Bird Watcher's Digest, The Living Bird,* and the *Living Bird Quarterly.* She is illustrating the New York State Breeding Bird Atlas.

Karen is preparing a major exhibition on the life of the Atlantic Puffin (*Fratercula arctica*)

and related seabirds. Her field work has taken her to Eastern Egg Rock and Matinicus Rock off the coast of Maine, and to Great Island in the Witless Bay Seabird Sanctuary off the coast of New foundland. A month of valuable observations, field sketches and photographs on Great Island helped create the Razorbill painting that won the Sutton Award.

## STUDENT MEMBERSHIP AWARDS IN THE WILSON ORNITHOLOGICAL SOCIETY FOR 1986

Student Membership Awards in the Wilson Ornithological Society have been made available from the general funds of the society to recognize students who have the potential to make significant contributions to ornithology. The following students have been selected by the Student Membership Committee for awards this year: Michael E. Barnes, Kansas State Univ.; Constance J. Boardman, California State Univ.; Stephen C. Brown, Univ. Michigan; David A. Buehler, Virginia Tech; Linda A. Caine, Univ. Florida; John P. Carroll, Univ. North Dakota; Greg H. Farley, Kansas State Univ.; Thomas P. Fitch, Idaho State Univ.; Fernando G. Garcia, Programa Fauna de Mexico; Nicholas W. Gard, Macdonald College, Quebec; Dale E. Gawlik, Winthrop College; Michael T. Green, Univ. North Carolina; Floyd E. Hayes, Univ. Michigan; Gloria E. Jacoby, Univ. Kentucky; Paula K. Kleintjes, California Polytechnic State Univ.; Michael J. Kolasa, Northern Michigan Univ.; Natasha B. Kotliar, Univ. New Mexico; Keven J. Kritz, Univ. Missouri; Darrell E. Land, Univ. Florida; Michael P. Losito, Auburn Univ.; Craig D. Olawsky, Texas Tech Univ.; James C. Ozier, Univ. Georgia; Bradley E. Sample, Univ. Delaware; Birgit C. Schultz, McGill Univ., Quebec; Dave Shutler, Macdonald College, Quebec; Alexander P. Smith, Univ. North Carolina.

Student Membership Committee, Wilson Ornithological Society—Thomas C. Grubb, Charles F. Leck, Roland R. Roth, and Richard N. Conner (chair).

*Wilson Bull.*, 98(2), 1986, pp. 335–336

# INFORMATION FOR AUTHORS

*The Wilson Bulletin* publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

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Authors of accepted papers are urged to submit voucher photographs of their work to Visual Resources for Ornithology (VIREO) at the Academy of Natural Sciences of Philadelphia. Accession numbers from VIREO will then be published within appropriate sections of the paper to facilitate access to the photographs in subsequent years.

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The editor welcomes queries concerning style and format during your preparation of mss for submission to the *Bulletin.*—Keith L. Bildstein, Editor.

This issue of *The Wilson Bulletin* was published on 6 June 1986.

# The Wilson Bulletin

*Editor* Keith L. Bildstein
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Winthrop College
Rock Hill
South Carolina 29733

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## CONTENTS


WAX DIGESTION IN WILSON'S STORM-PETREL ..... *Bryan S. Obst* 189

FORAGING PATTERNS OF FOREST BIRDS: MALE-FEMALE DIFFERENCES ..... *Richard T. Holmes* 196

THE STRUCTURE OF A FOREST BIRD COMMUNITY DURING WINTER AND SUMMER
*Michael L. Morrison, Kimberly A. With, and Irene C. Timossi* 214

NEST-SITE CHARACTERISTICS OF OPEN-NESTING BIRDS IN RIPARIAN HABITATS IN IOWA
*Dean F. Stauffer and Louis B. Best* 231

ASPECTS OF THE BIOLOGY OF THE HORNED SCREAMER IN SOUTHWESTERN COLOMBIA
*Luis G. Naranjo* 243

SOME ASPECTS OF THE BREEDING BIOLOGY OF RED-WINGED BLACKBIRDS IN ALASKA
*A. David McGuire* 257

AGE-SPECIFIC FORAGING ABILITY AND THE EVOLUTION OF DEFERRED BREEDING IN THREE SPECIES OF GULLS ..... *Alexis A. E. MacLean* 267

THE EFFECTS OF MUSCLE BIOPSY ON SURVIVAL AND CONDITION IN WHITE-THROATED SPARROWS
*David F. Westneat* 280

GENERAL NOTES

DISTRIBUTION OF FOOD WITHIN BROODS OF BARN SWALLOWS
*W. Bruce McGillivray and Howard Levenson* 286

SPECIES-AREA RELATIONSHIP OF MIGRANTS IN ISOLATED WOODLOTS IN EAST-CENTRAL ILLINOIS ..... *John G. Blake* 291

INCUBATION CONTINUITY AND THE ADVANTAGE OF CRYPTIC EGG COLORATION TO MOURNING DOVES ..... *David Westmoreland and Louis B. Best* 297

EFFECTS OF OLD NESTS ON NEST-SITE SELECTION IN BLACK-CROWNED NIGHT-HERONS AND SNOWY EGRETS ..... *William E. Davis, Jr.* 300

THE USE OF TAPE-RECORDED CALLS TO COUNT VIRGINIA RAILS AND SORAS
*Rex R. Johnson and James J. Dinsmore* 303

FOOD ROBBERY OF WINTERING RING-NECKED DUCKS BY AMERICAN COOTS
*James F. Bergan and Loren M. Smith* 306

POLYGYNY IN THE EVENING GROSBEAK ..... *Barbara A. Fee and Marc Bekoff* 308

NESTING TRIOS OF MOURNING DOVES ..... *David E. Blockstein* 309

SUPERNUMERARY ADULTS FEEDING WILLOW FLYCATCHER FLEDGLINGS
*Michael D. Stafford* 311

BROOD ADOPTION BY A MALE BLACK-CAPPED CHICKADEE ..... *James L. Howitz* 312

BROWN THRASHERS RESPOND TO CALLS OF NORTHERN MOCKINGBIRD NESTLINGS
*Kimberly G. Smith* 313

BEHAVIOR OF A POLYGYNOUS YEARLING YELLOW WARBLER
*Mary L. Reid and Spencer G. Sealy* 315

RANGE EXTENSION OF CAYENNE TERNS ON THE PUERTO RICO BANK
*Fred C. Schaffner, Robert L. Norton, and John Taylor* 317

DOWNY WOODPECKER FEEDS ON INSECTS IN A SPIDER'S WEB ..... *Harry M. Tiebout, III* 319

NEST-BUILDING BEHAVIOR IN A YOUNG AMERICAN ROBIN ..... *Pamela C. Rasmussen* 319

THE HISS-DISPLAY OF NESTLING BLACK-CAPPED CHICKADEES IN CAPTIVITY
*Karen M. Apel and Charles M. Weise* 320

NESTLING GREAT CRESTED FLYCATCHER PARASITIZED BY LARVAL FLY (*PROTOCALLIPHORA HIRUDO*) ..... *Barrett A. Garrison, Catherine Vouchilas, and Dean F. Stauffer* 321

ORNITHOLOGICAL LITERATURE ..... 322

ANNOUNCEMENTS ..... 195, 333

INFORMATION FOR AUTHORS ..... 335

# The Wilson Bulletin

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The *Herpsilochmus pileatus* complex, including the Ash-throated Antwren, *H. parkeri,* sp. nov. (upper pair) and (left to right) the White-browed Antwren, *H pileatus,* the Black-capped Antwren, *H atricapillus,* and the Yellow-bellied Antwren, *H. motacilloides.* Males are above, females below. From a mixed-media painting by John P. O'Neill.

THE WILSON BULLETIN

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# A NEW SPECIES OF ANTWREN (FORMICARIIDAE: *HERPSILOCHMUS*) FROM PERU, WITH COMMENTS ON THE SYSTEMATICS OF OTHER MEMBERS OF THE GENUS

TRISTAN J. DAVIS AND JOHN P. O'NEILL[1]

ABSTRACT.—In northern Peru during 1983 we collected specimens of an undescribed taxon of antwren of the poorly known genus *Herpsilochmus* that is best described as a new species, which we call *H. parkeri*, the Ash-throated Antwren. The new species may replace *H. axillaris* ecologically at similar elevations in the eastern Andes of northern Peru. Based on plumage patterns, the genus *Herpsilochmus* can be divided into four or five groups: *H. parkeri* appears to belong to the group consisting of all of the taxa that have previously been considered conspecific with *H. pileatus* (nominate *pileatus, atricapillus,* and *motacilloides*). These taxa, including *parkeri,* have allopatric distributions except for the complete overlap of the range of nominate *pileatus* within the range of *atricapillus.* Habitat differences apparently exist among the taxa: *parkeri* and *motacilloides* inhabit humid upper tropical and subtropical forest in the Andes, *pileatus* inhabits caatinga, and *atricapillus* prefers dry forest in southern South America. Plumage differences between the taxa are as great as are those between other species pairs within the genus *Herpsilochmus* whose ranges apparently overlap with no evidence of interbreeding. Owing to the lack of evidence of intergradation between *pileatus* and *atricapillus* where their ranges overlap, these taxa should be considered separate species. Upon consideration of the differences in habitat, plumage, and vocalizations that exist between *atricapillus, motacilloides,* and *parkeri,* it seems best to treat each of these taxa as separate species until further data are available. *Received 3 June 1985, accepted 11 Jan. 1986.*

The genus *Herpsilochmus* (Formicariidae), as currently recognized (Peters 1951; Meyer de Schauensee 1966, 1970), consists of nine species of antwrens, many of which are little known in the field and poorly repre-

[1] Museum of Zoology and Dept. Zoology and Physiology, Louisiana State Univ., 119 Foster Hall, Baton Rouge, Louisiana 70803-3216.

sented in most collections. In fall 1983, while on an expedition for the Louisiana State University Museum of Zoology (hereafter LSUMZ) in northern Peru, we obtained a series of an undescribed taxon of *Herpsilochmus* antwren. Our investigations of the relationships of this new form led us to review the species limits and taxonomy of the *H. pileatus* complex (*H.* "*p.*" *pileatus, H.* "*p.*" *atricapillus,* and *H.* "*p.*" *motacilloides*). In this paper we propose that each of these taxa is best considered a full species.

The new antwren is most closely related to the taxa included in *H. pileatus* but represents a distinct new species that we propose to call

## ***Herpsilochmus parkeri*** sp. nov.

ASH-THROATED ANTWREN

HOLOTYPE.—Louisiana State University Museum of Zoology No. 116908; adult male from ca 15 km by trail northeast of Jirillo on the trail to Balsapuerto, 06°03′S, 76°44′W, 1350 m, Department of San Martín, Peru, 20 November 1983; collected by Tristan J. Davis, original no. 3051.

DIAGNOSIS.—A relatively large (ca 11.5–13 cm total length), sexually dimorphic antwren, the males of which most closely resemble the males of *H.* "*pileatus*" *atricapillus* of southern South America by their size, unspotted rectrices (throughout this paper, a spotted tail refers to one that has the inner webs of the innermost rectrices marked along their edge with black and white alternating, instead of having the white along the edge continuous [="unspotted"]; when observed from above, the former appears as a row of spots along the center of the tail), unmarked chest, and gray and white underparts. Males distinguished from *atricapillus* by having a black loral spot instead of a thin grayish black eyeline between eye and bill, an ash-gray instead of white throat, and darker gray sides, flanks and chest (Frontispiece, Fig. 2). Distinguished from *H.* "*p.*" *motacilloides* by lack of yellowish wash on breast and belly, more black and white in the interscapulars, darker gray breast, sides and flanks, and ash-gray as opposed to whitish throat. Females like females of *H.* "*p.*" *atricapillus* but differ in having a darker buff throat, a bright buff instead of whitish eyebrow, a clear white instead of a buffy abdomen, buffy gray instead of buff flanks, and midback gray only slightly tinged buff, lacking the strong olive-buff tones present on the backs of *atricapillus.* Females also similar to females of *H. dorsimaculatus* but differ in having a long, unspotted instead of a rather short, spotted tail and an unmarked, grayish back instead of a grayish back broadly striped with black and white.

DISTRIBUTION.—So far, known only from the type locality east-southeast of Moyobamba in the Department of San Martín, northern Peru (Fig. 1).

DESCRIPTION OF HOLOTYPE.—Crown, extending from bill to upper midback, Jet Black (capitalized color names from Smithe 1975). Eyebrow, extending from the side of the base of the bill passing just over the eye and extending to the side of the back of the crown, pale grayish white. Feathers just below eye pale grayish white finely edged with gray, near Medium Neutral Gray. Lores and line extending from behind eye, below eyebrow as far as the hind-crown, Jet Black. Auriculars pale grayish white, darkening slightly towards sides of neck. Chin pale grayish white. Throat and breast near Pale Neutral Gray, slightly intermixed with whitish. Sides of breast, sides, and flanks very close to Light Neutral Gray (slightly paler). Center of abdomen clear white. Undertail coverts grayish white. Back closest to Dark Neutral Gray, interscapulars along midback variously intermixed with Jet Black and white; Jet Black found on outer one-third to one-fourth of feathers, white usually found as a spot

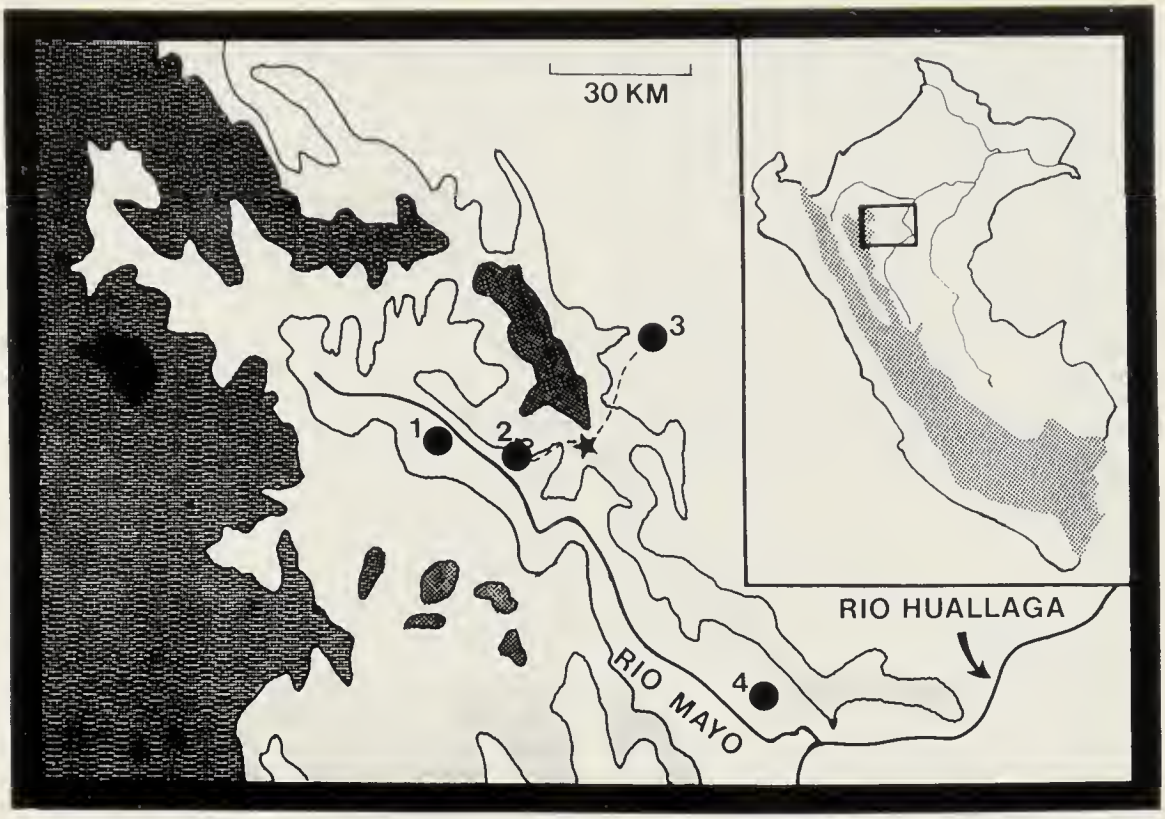


FIG. 1. Andes of northern Peru showing localities in the Río Mayo and Río Huallaga. 1. Moyobamba; 2. Jirillo; 3. Balsapuerto; 4. Tarapoto; star, type locality; dotted line, Jirillo-Balsapuerto trail (light stippling above 1000 m; dark stippling above 2000 m).

located on only one web about halfway down the length of the feather; a few of the feathers having some Jet Black lack any trace of white. Scapulars Blackish Neutral Gray to Jet Black broadly edged white on outer webs. Rump near Medium Neutral Gray. Upper tail coverts blackish Neutral Gray. Tail with rectrix numbers (numbering from the inside out on each side) 1, 4, and 5 (right), and 1, 5, and 6 (left); remaining rectrices missing. Rectrices white towards tips, black towards bases. Outermost rectrix with the most white (distal half white); each succesive rectrix thereafter has relatively less white than the previous one. Central rectrices (no. 1 left and right) black, narrowly tipped white: inner webs narrowly fringed white on basal three-fourths of feather. Wings Jet Black, browner towards tips of remiges. Remiges edged white on outer webs except at their bases; inner webs edged with white but edging wider than on the outer webs. Upper wing coverts Jet Black broadly tipped white forming three distinct wing bars, the uppermost quite small. Soft part colors in life: iris brown; tarsi and feet bluish gray; maxilla black; mandible medium gray, lighter at edges.

MEASUREMENTS OF HOLOTYPE.—Wing (chord) 55.6 mm; tail 56.6 mm; culmen from base 16.5 mm; tarsus 17.5 mm; weight 11.5 g.

DESCRIPTION OF FEMALE.—Forehead orangish Cinnamon. Crown, extending from just above eyes to upper midback, between Sepia and Jet Black; some feathers with patch of white on one web forming elongated streaks on crown; a few feathers of forecrown with orangish Cinnamon shafts. Eyebrow extending from side of base of bill passing just over the eye and extending to the side of the back of the crown, lores, auriculars, and area just below eye between Clay Color and Yellow Ocher (feathers in area just below eye lightly edged Medium Neutral Gray). Line extending from behind eye beneath eyebrow between Sepia and Jet Black. Chin, throat, and breast close to Yellow Ocher (slightly grayish), throat

FIG. 2. A. Hand-held adult male *H. parkeri*. B. Tall forest understory at type locality.

slightly paler. Flanks and undertail coverts Pale Neutral Gray with a slight buffy wash. Abdomen white. Sides of breast and neck dull grayish Clay Color extending dorsally onto upper back forming an almost complete nuchal collar, broken in the middle by the thin black extension of the crown. Back Medium Neutral Gray, upper back lightly washed with ochraceous; a few feathers of the midback have their webs with black spots on them and some have very pale grayish white shafts with the same color on the nearby vanes; this pattern is reminiscent, although much reduced, of the coloration of the back in the males of the species. Inner webs of scapulars Dark Neutral Gray, outer webs Jet Black, the latter broadly edged white. Rump and upper tail coverts Medium Neutral Gray. Tail and wings similar to males.

SPECIMENS EXAMINED.—*H. parkeri*: Peru: San Martín, 4 ♂♂ and 4 ♀♀ (LSUMZ), 1 ♂ skeleton (LSUMZ), 1 ♂ in alcohol (LSUMZ). *H.* "*pileatus*" *pileatus*: Brazil: Bahia, 1 ♂ ([AMNH=] American Museum of Natural History), 2 ♀♀ (AMNH), 1 sex ? (♂ by plumage) ([BM=] British Museum). *H.* "*pileatus*" *atricapillus*: Brazil: Bahia, 1 ♂ (AMNH); Pernambuco, 1 ♂ (AMNH), 1 ♀ (AMNH); Goiás, 1 ♂ (LSUMZ), 1 ♀ (LSUMZ); "Pianky" (probably Piauí), 1 ♀ (AMNH); Bolivia: Chuquisaca, 1 ♂ ([ANSP=] Academy of Natural Sciences of Philadelphia); "Chiquitos," 1 ♀ (LSUMZ); Santa Cruz, 8 ♂♂ ([FMNH=] Field Museum of Natural History, LSUMZ), 4 ♀♀ (FMNH, LSUMZ); Tarija, 1 ♂ (AMNH), 2 ♀♀ (ANSP). *H.* "*pileatus*" *motacilloides*: Peru: Junín: Utcuyacu, 1 ♂, 1 ♀ (AMNH); Pasco: Pichis Trail (formerly in Junín), 2 ♂♂, 1 ♀ (ANSP), Santa Cruz, 1 ♂, 1 ♀ (LSUMZ), Cushi, 1 ♂, 1 ♀ (LSUMZ). *H. sticturus* (excluding *dugandi*): British Guiana, 2 ♂♂, 1 ♀ (AMNH); Venezuela, 1 ♀ (AMNH). *H.* "*sticturus*" *dugandi*: Peru, 1 ♂, 1 ♀ (LSUMZ). *H. stictocephalus*: Guyana, 1 ♂, 2 ♀♀ (AMNH). *H. dorsimaculatus*: Brazil, 2 ♂♂, 2 ♀♀ (AMNH). *H. roraimae*: Venezuela, 2 ♂♂, 1 ♀ (AMNH); "Roraima," 1 ♀ (AMNH). *H. pectoralis*: Brazil, 2 ♂♂, 1 ♀ (LSUMZ). *H. longirostris*: Brazil, 4 ♂♂, 2 ♀♀ (LSUMZ, AMNH); Bolivia: Dept. Beni, Río Iténez, 1 ♂ (AMNH;

first report of the species in Bolivia). *H. axillaris*: Peru, 1 ♂, 1 ♀ (LSUMZ). *H. rufimarginatus*: Panama, 1 ♂, 1 ♀ (LSUMZ); Venezuela, 1 ♂, 1 ♀ (LSUMZ); Brazil, 1 ♂ (LSUMZ); Peru, 2 ♂♂, 3 ♀♀ (LSUMZ); Bolivia, 1 ♂, 2 ♀♀ (LSUMZ); Paraguay, 1 ♂ (LSUMZ).

ETYMOLOGY.—We are pleased to name this species after our good friend Theodore A. Parker III, who, after more than a decade of studying neotropical birds in both the field and the museum, is unrivaled in his knowledge of the natural history of South American avifauna. He eagerly shares his vast knowledge, and in this way he influences many of those interested in neotropical birds, both professionals and lay-people alike.

The proposed English name, Ash-throated Antwren, refers to the light grayish throat of the males of the new species; this is one of the characteristics that distinguishes it from closely related congeners.

## REMARKS

*Variation in the type series.*—Only slight variation in plumage coloration is apparent within the series. Males vary in the amount of black and white mixed in the interscapulars. White is usually more predominant than the black; black on the interscapulars varies from a few centrally located blotches to rather extensive markings over much of the midback. The holotype has slightly more black in the interscapulars than the other three males. This individual variation in the amount of black and white in the interscapulars seems to be typical in those species of *Herpsilochmus* in which such interscapular markings occur. Perhaps this variability is age related (see below). Almost no variation in female plumage coloration is apparent except for one adult female (LSUMZ, skull 100% pneumatized), which has the throat and breast a slightly paler shade of buff. Females also vary in the amount of white spotting on the crown. The two females with 100% ossified skulls have very little white on the crown, while the other two females have more extensive white spotting (these latter two have their skulls 10% and 90% ossified). There seems to be considerable variation in the extent of white spotting on the crowns of females with this trait in the genus *Herpsilochmus* as a whole. Some specimens show only a trace of the spotting while others show extensive white spotting. This variation may be age related, but more specimens with gonad and skull data are needed to confirm this. Descriptions of soft part colors vary only slightly in the new species. The color of the lower mandible is apparently darker in the males; the color in all four males was recorded as gray (one with a black tip and another lighter along cutting edge), whereas in all four females it was recorded as light gray (one lighter at edges). Descriptions of the color of the tarsi and feet (=toes) of the birds of both sexes were light gray, gray, dark gray, and blue-gray.

Two males and one female of the new species show what may be age-related plumage variations. A male collected by O'Neill on 27 October has its skull only 5% pneumatized. This bird's plumage is exactly as in the other 3 males (two with fully pneumatized skulls and one with the

skull 50% pneumatized) except in the following ways: the black and white in the interscapulars is reduced to a few small spots, the gray of the underparts is a lighter shade than in the other males, and the black loral spot is smaller. The male specimen with the 50% pneumatized skull (LSUMZ) also has a smaller loral spot and less black in the interscapulars than the two birds with skulls 100% pneumatized, but it is otherwise similar to them. Both of these specimens appear to have adult rectrices (rounded as opposed to slightly pointed in juvenal rectrices); the former specimen, however, was in the process of molting almost its entire tail, and only three rectrices are fully grown, and with at least one of these three appearing fresh. The latter specimen also lacks several of its rectrices, but there is no apparent sign of molt. These two specimens probably had already lost most, if not all, of their juvenal rectrices and had begun to grow the rounded rectrices of the adult plumage. A female collected on 1 November by Davis has its skull 10% pneumatized, and its ovary was only 3 × 1 mm and smooth.This individual's plumage is as in the three other female specimens (two with fully pneumatized skulls and one with its skull 90% pneumatized) except as follows: the rectrices are pointed as opposed to rounded, and the white of the belly is not as pure as in the other females, being slightly intermixed with pale buff towards the breast.

*Breeding and molt.*—None of the specimens was in breeding condition. The largest testis of any of the males was 3 × 1.5 mm, and the largest ovary of any of the females 6 × 3 mm, with the ova and the oviduct minute. Because all the specimens were collected from the end of October to late November, it may be that most breeding takes place during the drier part of the year (the dry season in the area is from about May to September or October), although much singing was heard throughout our stay. Two birds were in light to moderate body molt. Although no body molt was recorded in the remaining specimens, the rectrices of almost all of the specimens varied from lightly worn to heavily worn at the tips, especially in the females. The condition of the feathers leads one to suspect that the main part of the breeding season had just been completed, and the birds had not yet gone through a postbreeding molt. Six of the nine specimens obtained were apparently paired when collected; the three that were not known to be paired when collected include the female with the 10% pneumatized skull, the male with the 5% pneumatized skull, and a male that was netted.

*Habitat and ecology.*—Habitats at the only known locality for the new species are very heterogeneous. The Moyobamba Valley directly to the west of the mountain ridge is moderately xeric, owing to a partial rain-shadow effect. Our camp was situated at what appeared to be the upper elevational limit of the savanna-like habitat that characterizes much of that valley. This habitat was distributed only in scattered patches at 1350

m. There was also a distinct habitat, located mostly on ridges in the area, that resulted from the outcropping of sandy, poor-quality soils where vegetation was usually short (ca 4 m), extremely dense, and of low floristic diversity. A semistunted, more-diverse forest was also present and seemed to form a transition between the savanna-like vegetation and the tall cloud forest that was present in areas with good soil. The semistunted forest had a canopy height of ca 12 m, whereas the tall forest averaged 30–35 m in height. For more information on this locality and its avifauna, see Davis (1986).

*H. parkeri* was noted most commonly in the canopy and midlevels of the tallest forest. The undergrowth in this habitat was moderately open, the canopy was mostly closed, and epiphytes were common (Fig. 2B). The antwren was only slightly less common in the semistunted forest and was also found there from the midlevels of the forest to the canopy. The undergrowth in this latter habitat was extremely dense, and the canopy was only slightly closed; epiphytes there were extremely abundant. *H. parkeri* was recorded only once from the savanna-like habitat, where one male was netted in some low bushes at the surprisingly abrupt border between this habitat and the semistunted forest (the abrupt transition may be fire-maintained). The species was usually seen traveling in pairs in association with a mixed-species flock, and its song was heard quite often. Other species of birds noted in the same flocks with *H. parkeri* included, most commonly, *Myrmotherula schisticolor, Automolus ochrolaemus, Xiphorhynchus ocellatus, Xenops rutilans,* and *Hemitriccus rufigularis.*

Although the avifauna at this locality was very similar to the avifauna at another LSUMZ collecting locality almost directly across the Moyobamba Valley (Parker and Parker 1982), the only species of *Herpsilochmus* recorded at the latter site was *H. axillaris.* At a similar locality in the Department of Amazonas (east of La Peca) at a slightly higher elevation ca 180 km northwest of the type locality of the new species, an LSUMZ party also recorded only *H. axillaris.* At both of these localities *H. axillaris* was uncommon to rare. It is possible that *H. parkeri* is indeed truly restricted to the low mountain range east of Moyobamba, an isolated area with poor soil and low plant diversity, and is ecologically replaced elsewhere in northern Peru at similar elevations by *H. axillaris.* Of course it is possible that we overlooked the latter species at the locality where *H. parkeri* was common, but we doubt this because we spent a month there studying the avifauna.

Stomach contents of five individuals of *H. parkeri* were examined (LSUMZ Stomach Contents Collection). These stomachs contained a variety of insects, primarily Coleoptera (including Curculionidae and Coccinellidae, at least one of which was identified as a probable *Brachiacantha* sp. of the tribe Hyperaspini) and Hemiptera (both of which were present

in five stomachs), and Hymenoptera (present in four stomachs). Other insects identified in the stomachs but in lower frequencies than the previously mentioned taxa included Homoptera (including at least one Fulgoroidea), Formicidae, Orthoptera, Dermaptera, and one spider of the Araneae (probably Salticidae).

*Voice.*—The song of *H. parkeri* began with a series of 3–4 well-spaced notes followed by an accelerating and slightly descending rapid succession of notes that ran together towards the end and stopped abruptly; an entire song phrase lasted 3–4 sec. Songs of closely related *motacilloides* and *atricapillus* seem to differ in lacking the introductory component (pers. obs.; tape recordings in Library of Natural Sounds, Cornell University). The song of *atricapillus* differs additionally by becoming slower towards the end so that the terminal sequence is somewhat protracted. Songs of *pileatus* remain unknown.

*Systematic relationships.*—Four to five groups in the genus *Herpsilochmus* can be distinguished based on shared plumage patterns. The most differentiated taxa in the genus, *H. axillaris* and *H. rufimarginatus* (possibly two different "groups"), are both bright yellow below (unlike all other members of the genus) and have unspotted tails. The former inhabits cool upper tropical and subtropical forests in the Andes, whereas the latter inhabits mostly forested lowlands from Central America to Bolivia and Paraguay. Another group consists of *H. longirostris* and *H. pectoralis*; we consider these two species closely related because both male and female plumages are extremely similar and their ranges almost abut. A third group consists of those species in the genus that possess a tail that is spotted along the inner webs of the central rectrices. This group includes the following species: *H. sticturus* (including *dugandi*), *H. stictocephalus, H. dorsimaculatus,* and *H. roraimae.* The first two in this group are probably more closely related to one another than either is to any other member of the group. *H. roraimae* differs from all other members of this group in having a longer tail, consequently with more spots, and in having spots on both webs of the central rectrices instead of just on the inner webs. Some individuals of the other species in this group do show a hint of spots on the outer webs also. The last group includes the taxa that have been included in the species *H. pileatus.* For reasons discussed later, all three taxa within that species are best treated as distinct species. This last group can be distinguished as having a tail that lacks spots, with the central rectrices edged with white on their inner webs for most of their length; as lacking any distinct dark markings across the chest, and as having their underparts basically gray and white (1 taxon with a yellowish wash below). All except nominate *pileatus* can also be distinguished as having a relatively longer tail than do most other members of the genus (Table 1).

TABLE 1

SELECTED MEASUREMENTS (MM) OF THE SPECIES OF *HERPSILOCHMUS*

| Species | Culmen (from base) | | Wing chord | | Tail | | Tarsi | |
|---|---|---|---|---|---|---|---|---|
| | N | $\bar{x}$ (range) | N | $\bar{x}$ (range) | N | $\bar{x}$ (range) | N | $\bar{x}$ (range) |
| *parkeri* | 8 | 17.2 (16.5–17.6) | 8 | 54.7 (52.4–57.9) | 6 | 57.0 (55.7–58.3) | 8 | 18.2 (16.8–19.1) |
| *pileatus* | 4 | 15.5 (14.3–17.3) | 4 | 46.7 (43.0–49.8) | 3 | 44.1 (43.0–45.1) | 4 | 16.8 (15.6–17.2) |
| *atricapillus* | 21 | 16.15 (15.1–16.7) | 23 | 52.3 (49.0–56.0) | 20 | 52.5 (48.2–55.7) | 22 | 18.1 (16.5–18.9) |
| *motacilloides* | 10 | 16.0 (15.5–16.5) | 10 | 52.5 (50.5–54.5) | 10 | 53.6 (49.8–56.4) | 9 | 17.2 (16.4–18.1) |
| *sticturus* | 4 | 16.2 (15.9–16.4) | 4 | 46.7 (45.2–47.5) | 4 | 34.2 (33.6–35.3) | 4 | 15.8 (15.5–16.0) |
| "*s.*" *dugandi* | 2 | 16.2 (15.9–16.4) | 2 | 47.8 (46.5–49.1) | 2 | 34.5 (34.4–34.6) | 2 | 16.3 (15.7–16.8) |
| *stictocephalus* | 3 | 16.1 (15.9–16.3) | 3 | 46.8 (45.0–48.1) | 3 | 35.1 (34.7–35.4) | 3 | 15.6 (14.8–16.4) |
| *dorsimaculatus* | 4 | 16.7 (16.4–17.1) | 4 | 48.1 (46.6–51.3) | 4 | 39.9 (38.2–40.2) | 3 | 17.0 (16.5–17.4) |
| *roraimae* | 4 | 17.3 (16.8–17.9) | 4 | 53.3 (52.5–54.2) | 4 | 52.6 (51.6–54.7) | 4 | 18.4 (17.9–19.3) |
| *pectoralis* | 3 | 16.8 (16.1–17.3) | 3 | 51.2 (50.7–51.8) | 3 | 38.3 (38.1–38.6) | 3 | 19.6 (19.2–19.9) |
| *longirostris* | 21 | 19.0 (18.1–19.9) | 21 | 60.2 (57.9–62.6) | 20 | 54.2 (49.1–57.4) | 20 | 19.5 (18.8–21.2) |
| *axillaris* | 2 | 15.9 (15.3–16.5) | 2 | 51.8 (50.1–53.5) | 2 | 45.8 (45.5–46.1) | 2 | 16.7 (16.3–17.0) |
| *rufimarginatus* | 13 | 16.7 (15.7–17.4) | 13 | 50.0 (47.8–53.2) | 12 | 43.3 (37.4–48.5) | 13 | 18.1 (17.1–18.9) |

*H. parkeri,* based on plumage alone, best fits into the last group. The tail pattern in the new species is exactly as in the other members of the group. The plumage of the males in the new species closely resembles the male plumage of both *H.* "*pileatus*" *atricapillus* and *H.* "*pileatus*" *motacilloides.* The females of *H. parkeri* resemble the females of *H. dorsimaculatus* in that they both have a bright buff throat and breast contrasting with a white belly and grayish flanks, an ochraceous forehead, and a black crown with white spots. *H. dorsimaculatus* and *H. parkeri* are the only species in the genus that possess this particular color pattern, although there is a hint of this pattern (e.g., a pale buffy wash across the breast) in several other members of the genus. Otherwise, *H. dorsimaculatus* and *H. parkeri* are very different. *H. parkeri* females, with their long, unspotted tails and unmarked grayish backs, lack the spotted and relatively short tail of *H. dorsimaculatus,* and also lack the boldly striped back characteristic of the latter species. Additionally, the females of *H. parkeri* share similarities with the females in the *H. pileatus* group including similarly patterned, relatively long tails, and unmarked grayish backs, in addition to a similar overall body size and shape. For the above reasons, we believe that *H. parkeri* is most closely related to the taxa previously included in *H. pileatus.*

## SYSTEMATICS OF THE *HERPSILOCHMUS PILEATUS* COMPLEX

The three taxa that have been included in *Herpsilochmus pileatus* (nominate *pileatus, motacilloides,* and *atricapillus*) are quite distinct from one another (Frontispiece), but, along with *H. parkeri,* appear to form a "natural" group. The distinguishing and shared plumage characteristics of these four taxa are listed in Table 2. The males show fewer differences in plumage coloration between taxa than do the females, but this is typical among many closely related taxa of Formicariidae. Selected measurements of these four taxa and the remaining species in the genus *Herpsilochmus* are given in Table 1. Of the four taxa involved in the *H. pileatus* complex, *atricapillus* and *pileatus* appear to be the most similar in plumage coloration, while *atricapillus, motacilloides,* and *parkeri* are more similar to each other in size and proportions than any of these is to *pileatus* (although *parkeri* averages larger in all characters measured) (Table 1). In both sexes tail length seems to be the best distinguishing character and can serve to distinguish *pileatus* from similarly plumaged *atricapillus,* as well as *motacilloides* and *parkeri,* with no apparent overlap (Naumberg 1939) (Table 1).

These three taxa and *H. parkeri* are all essentially allopatric: *pileatus* inhabits a small portion of eastern Brazil; *atricapillus* occurs from eastern Bolivia east, south of Amazonia, to eastern Brazil; *motacilloides* inhabits

TABLE 2

SELECTED CHARACTERS OF MEMBERS OF THE *HERPSILOCHMUS PILEATUS* SPECIES COMPLEX

| Species | Sex | Lores | Throat | Midbresat | Belly | Forehead | Crown | Back | Neck |
|---|---|---|---|---|---|---|---|---|---|
| *pileatus* | ♂ | Whitish | White | White | White | Black | Black | Gray mixed black and white | Gray |
| | ♀ | Whitish | White | White (rarely with buff tinge) | White tinged buff near vent and flanks | Blackish (tinged buff in some specimens) | Blackish with pale edges (scalloped effect) | Gray tinged brownish-olive | Gray |
| *atricapillus* | ♂ | Whitish | White | White-pale gray | White | Black | Black | Gray mixed black and white | Gray |
| | ♀ | Whitish | Buff-very pale buff | Buff | Buff-very pale buff | Ochraceous | Black with white elongated spots | Gray tinged olive-buff | Gray tinged buff near breast |
| *motacilloides* | ♂ | Black | White | White washed yellow | White washed yellow | Black | Black | Gray mixed black and white | Gray |
| | ♀ | Black | White | White washed yellow | White washed yellow | Ochraceous | Black with white elongated spots | Gray tinged olive-buff | Gray |
| *parkeri* | ♂ | Black | Pale gray | Pale gray | White | Black | Black | Gray mixed black and white | Gray |
| | ♀ | Buffy-white | Buff | Buff | White | Ochraceous | Black with white elongated spots | Gray | Gray tinged dull buff encircling neck |

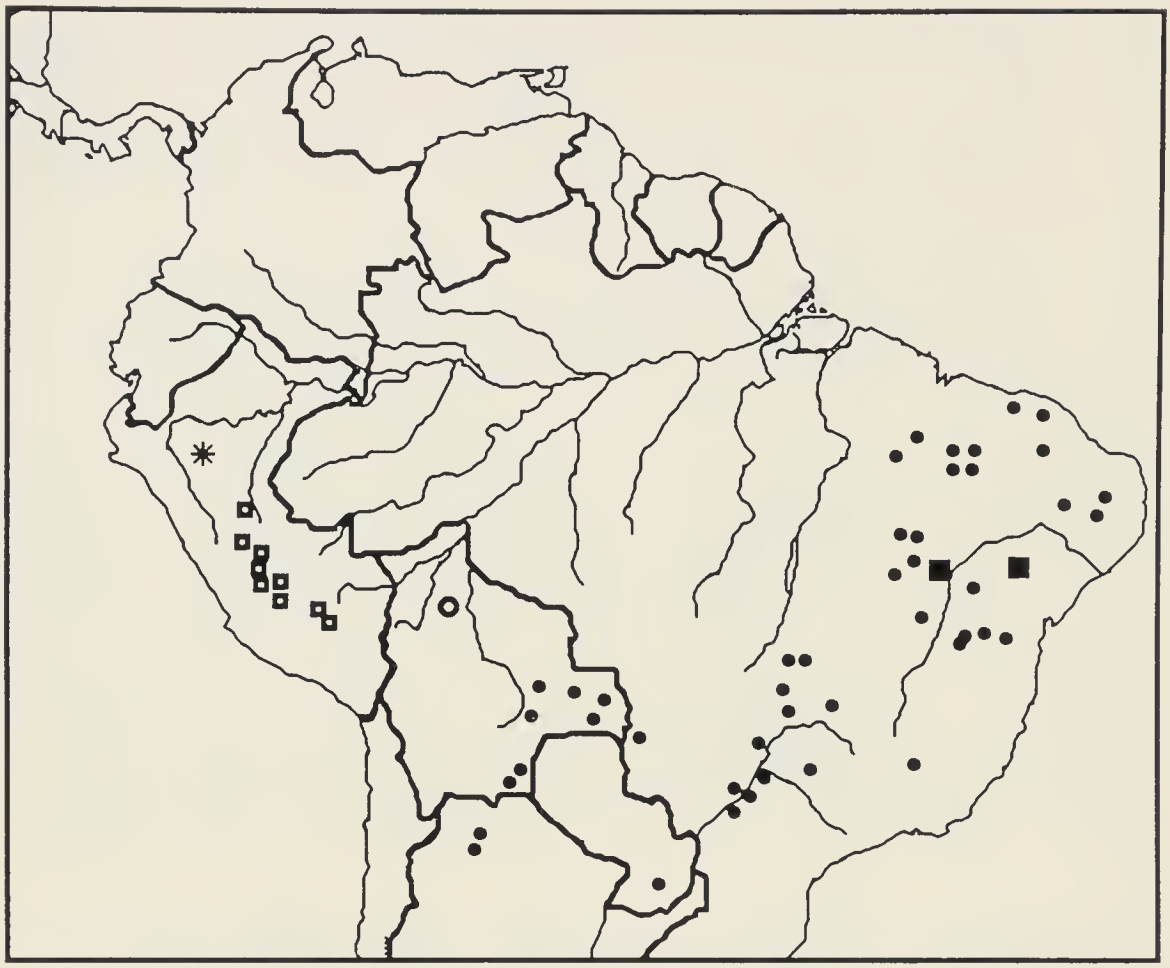

FIG. 3. Map of the distribution of members of the *Herpsilochmus pileatus* species complex. Large, solid squares: *pileatus*; small squares with open dot: *motacilloides*; asterisk: *parkeri*; small solid circles: *atricapillus*; large open circle: sight record of *atricapillus* by Remsen (in press).

central and southern Peru; and *H. parkeri* appears to be restricted to a small portion of northern Peru. Although nominate *pileatus* and *atricapillus* are essentially allopatric in that they have not been collected at the same locality, they are known to occur within 50 km of each other (Naumberg 1935, 1939), and localities of *atricapillus* are known that essentially surround the two known localities of *pileatus*. Thus, it actually appears that their ranges may overlap (Fig. 3).

In addition to the morphological and plumage differences that these four taxa exhibit, apparent differences exist in their preferred habitats. Nominate *pileatus* and *atricapillus* both are found in eastern Brazil where *pileatus* was said to inhabit caatinga forest (Naumberg 1939), a specialized forest type found in northeast Brazil from Rio Grande do Norte to southern Bahia, characterized by deciduous, thorny scrubland with many cacti and other succulents with the ground more or less open (Meyer de Schauensee 1970). In this region of Brazil, *atricapillus* was said to inhabit a habitat with dense underbrush and very little high forest (Naumberg

1939). J. V. Remsen (field notes, LSUMZ) found *atricapillus* to be fairly common in fairly tall deciduous forest in the Department of Santa Cruz, Bolivia, especially along a river where the trees tended to have more leaves, the canopy was variable, the undergrowth was dense with many ferns, there was no moss on the trees (only dried lichens), and epiphytes were virtually nonexistent. Although it appears that *pileatus* and *atricapillus* have ranges that essentially overlap, these two taxa may replace each other by habitat. Both known localities of *pileatus* are in caatinga, whereas the closest localities of *atricapillus* are in more humid deciduous forest; however, a few localities of *atricapillus* more distantly located from the localities of *pileatus* are also in caatinga (Naumberg 1935, 1939). In contrast to these habitat types, the habitat of both *motacilloides* and *parkeri* is dense, tall, evergreen cloud forest with heavy moss and epiphytic growth along the humid slopes of the Peruvian Andes in the Upper Tropical and Subtropical "zones." *H. parkeri* was found only at 1350 m even though elevations down to 750 m were studied intensively in the same range of foothills. Southeast Peruvian *motacilloides* has been recently collected at elevations of over 2000 m in the Andes (LSUMZ), but a few older specimens have localities of less than 1000 m. Both *pileatus* and *atricapillus* are more typical of elevations below 1000 m (Naumberg 1935, 1939; LSUMZ).

Vocalizations of different species within this genus are similarly structured. Nonetheless, the song of *parkeri* differs distinctively from the song of *motacilloides,* one of the taxa most closely related to *parkeri* and the one nearest to it geographically. The song of *atricapillus* differs from both *motacilloides* and *parkeri.* At present, however, lack of sufficient data on the vocalizations of the members of the genus precludes emphasizing vocalizations in determining the specific status of the taxa in question. Such an analysis must wait at least until vocalizations of *parkeri* are available and playback experiments between the taxa can be performed.

Due to the equivocal distribution of *pileatus* with respect to that of *atricapillus* and the lack of evidence of intergradation, these two taxa should be considered separate species. The classification of the remaining two taxa (*motacilloides* and *parkeri*) with respect to *atricapillus* is more difficult. Although Zimmer (1932) felt that *pileatus* and *atricapillus* were more closely related to each other than either was to *motacilloides,* we perceive that the latter two are almost equally differentiated from the nominate *pileatus.* Since *atricapillus, motacilloides,* and *parkeri* are completely allopatric, they could well be considered to be conspecific. Direct application of the biological species concept is difficult with allopatric populations (Mayr 1963), and degrees of morphological, biochemical, or behavioral differentiation must be used to determine specific status of such isolated taxa. Even so, such classifications remain tentative pending

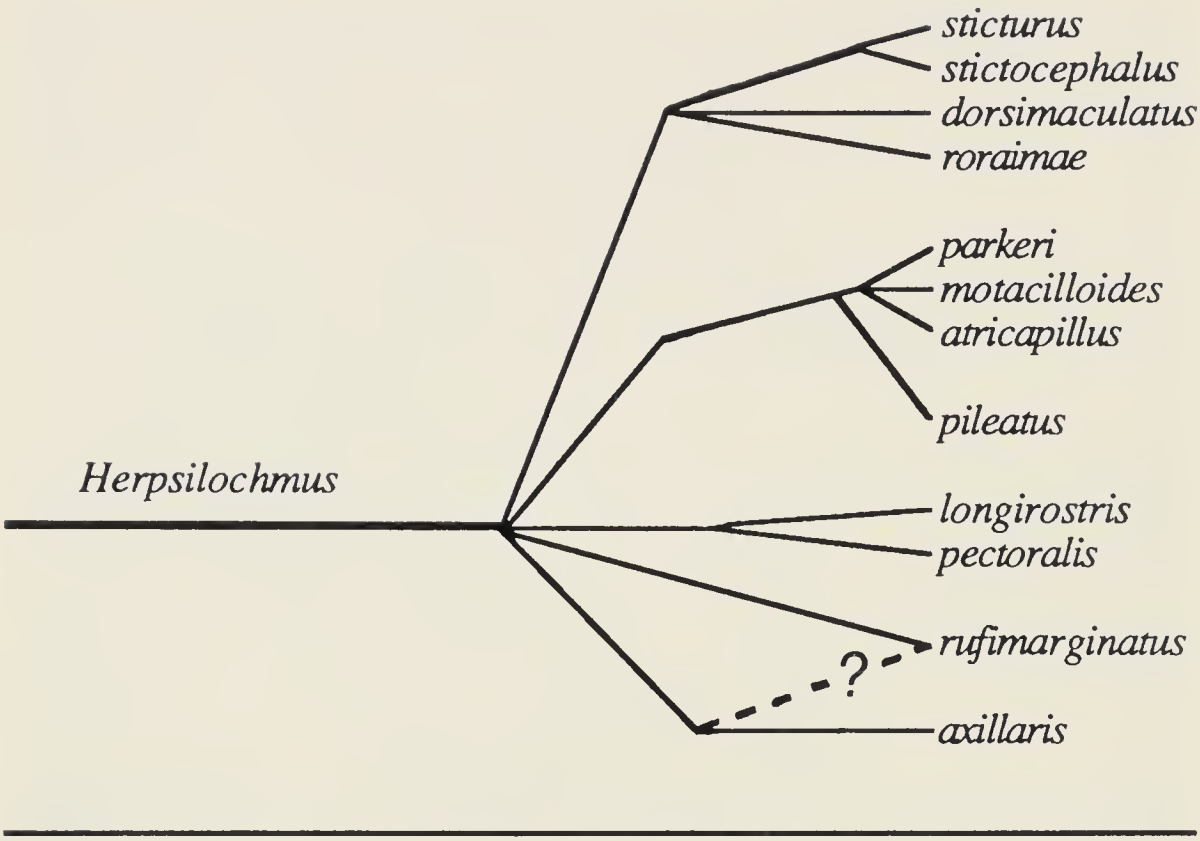


FIG. 4. Hypothetical relationships within the genus *Herpsilochmus*; dotted line indicates possible closer relationship between *rufimarginatus* and *axillaris*.

further knowledge of the natural histories of the taxa. Differences in plumage are as great between these taxa as are differences between other species pairs within the genus *Herpsilochmus* (i.e., *H. sticturus* and *H. stictocephalus,* and *H. longirostris* and *pectoralis*; as well as *atricapillus* and *pileatus* as already discussed). At least two of these pairs consist of species that are known to occur in the same general areas with no apparent interbreeding. In addition to differences in plumage, habitat preferences and vocal differences between *atricapillus* and *motacilloides-parkeri* also exist, as mentioned above. We perceive that given the above differences, *atricapillus* should also be considered specifically distinct from *motacilloides* and *parkeri.*

Even with the separation of *atricapillus* as a distinct species, there remains the possibility of treating *motacilloides* and *parkeri* as conspecific. These two taxa are separated from each other by ca 500 km of apparently suitable habitat for both species. Although there are few localities that have been collected at the appropriate elevations between the known ranges of these two taxa, only *H. axillaris,* an unrelated taxon, has been

found at such localities (e.g., Afluente, Department of San Martín [Parker and Parker 1982]). The known range of *motacilloides* extends from the Department of Huánuco to the central portion of the Department of Cuzco, a span of about 450 km. Specimens of *motacilloides* from the nearest localities to the known locality of *parkeri* show no trends toward characteristics of the latter taxon and are essentially identical to specimens of *motacilloides* from the southernmost localities. A single specimen of *motacilloides* from the Cordillera Vilcabamba, Department of Cuzco, does show less of a yellowish wash below than any of the other specimens of *motacilloides* we have examined, but it is otherwise identical to the rest of the series. Therefore, until additional information is available from geographically intermediate populations (if there are any), it seems best to consider *motacilloides* and *parkeri* as separate species. The resulting classification, recognizing *H. pileatus, H. atricapillus, H. motacilloides,* and *H. parkeri,* is consistent with respect to the species limits within the rest of the genus (Fig. 4). Although these four species are obviously closely related, we hesitate to classify them formally in a single superspecies until the ranges of *H. pileatus* and *H. atricapillus* are better known. The type of distribution that these four species show may be the result of withdrawal of a widespread ancestral form into isolated pockets of suitable habitat during the climatic changes of the Plio-Pleistocene, whereupon several disjunct populations differentiated from the others. Such a model has been hypothesized by Haffer (1974) for numerous taxa in lowland South America and has received support from studies of several groups of birds, especially tyrannids (Short 1975; Fitzpatrick 1976, 1980; Fitzpatrick and O'Neill 1979).

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## COLOR PLATE

The Frontispiece painting has been made possible by an endowment established by George Miksch Sutton. The painting is by J. P. O'Neill.

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# NESTING SUCCESS AND PRODUCTIVITY OF HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

WILLIAM H. BALTOSSER[1]

ABSTRACT.—Predation was the major source of nest failure for hummingbirds studied in southwestern New Mexico and southeastern Arizona, accounting for nearly 80% of all failed nest attempts. Predation on eggs was responsible for just over 70% of all losses attributed to predation; predation on nestlings accounted for <30% of the losses. Nest failures resulting from abandonment, structural failure, and infertility were low and similar to that found in other studies dealing with altricial young. On an annual basis, nesting success ranged from 0% for Costa's Hummingbirds (*Calypte costae*) in 1976 and 1980, to 80% for Broad-billed Hummingbirds (*Cynanthus latirostris*) in 1977. Significant differences in egg and nestling survival between early and late nests were found for Black-chinned Hummingbirds (*Archilochus alexandri*) in one of the three study areas. Average productivity (number of young fledged per female), based on data from all years and each study area, ranged from 0.16 ± 0.27 [SD] young per female for Costa's Hummingbirds to 2.32 ± 0.08 for Broad-billed Hummingbirds. Productivity for Black-chinned Hummingbirds, the most numerous of the five species studied, averaged 1.16 ± 0.87, while that of Violet-crowned Hummingbirds (*Amazilia violiceps*) averaged 1.43 ± 0.02. Productivity for Magnificent Hummingbirds (*Eugenes fulgens*), which nested only during 1976, was 1.16 young per female. Results of the present study are consistent with those of previous studies that have dealt with nesting female hummingbirds, and suggest that predation and productivity are more generalized than might be expected based on the range of habitats occupied. *Received 22 July 1985, accepted 29 Jan. 1986.*

Most studies of hummingbirds have concentrated on males or on the coevolution of plant pollinator systems, optimal foraging and energetics, territoriality, or on the organization of tropical communities. The few studies that have examined the ecology of nesting female hummingbirds in detail include those by Pitelka (1951a, b), Legg and Pitelka (1956), Calder (1973), Stiles (1973), Carpenter (1976), and Calder et al. (1983).

This paper presents the findings of a portion of a larger study (Baltosser 1978, 1983) that focused on the nesting ecology of female hummingbirds in southwestern New Mexico and southeastern Arizona. Here I (1) discuss the relative importance of predation and other sources of nest failure in terms of how they affected the nesting success and productivity of Black-chinned (*Archilochus alexandri*), Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), Costa's (*Calypte costae*), and Magnif-

[1] Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 (Present address: 5022 La Cienega NW, Albuquerque, New Mexico 87107).

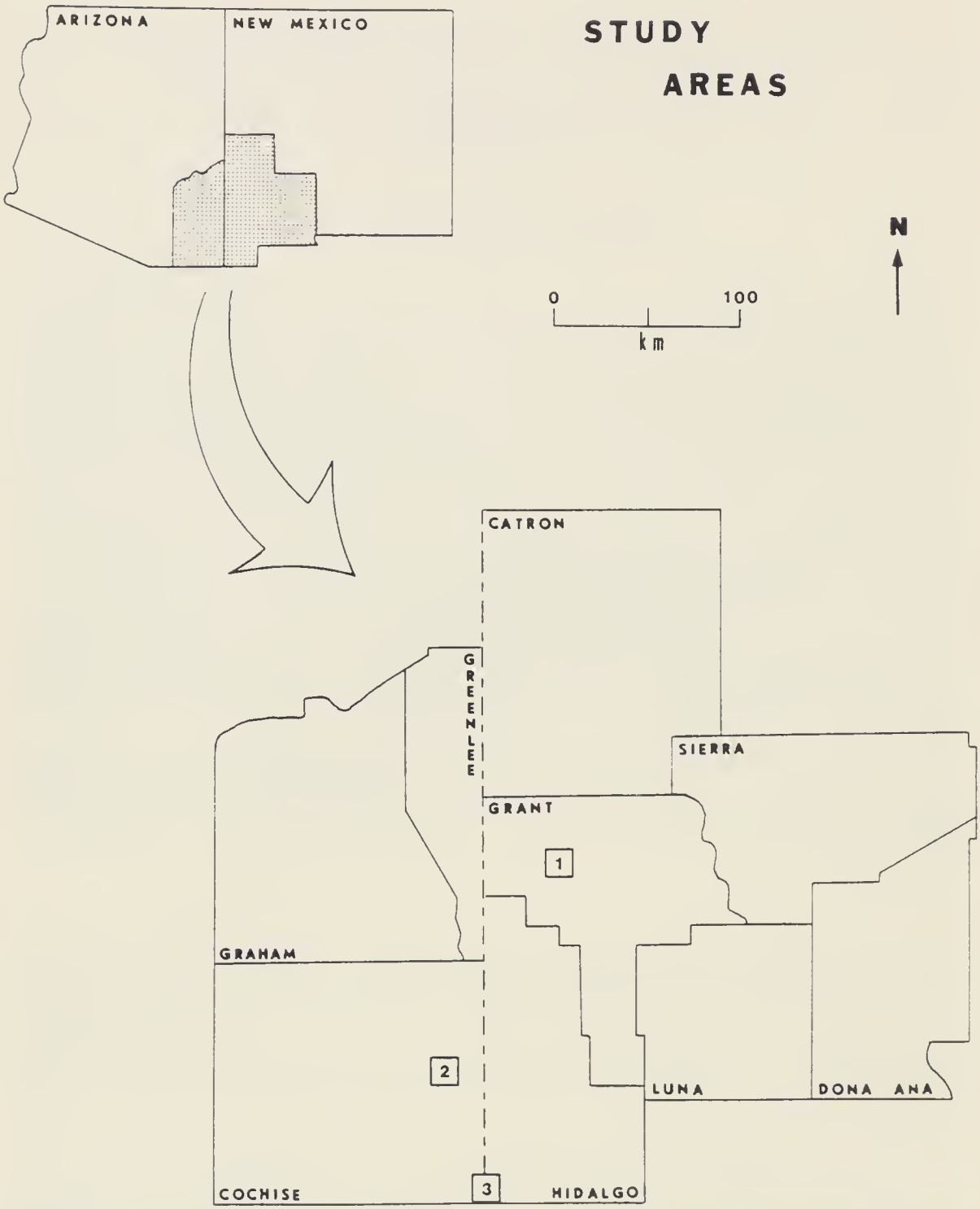


FIG. 1. Locations of the Cliff (1), Rucker Canyon (2), and Guadalupe Canyon (3) study areas.

icent (*Eugenes fulgens*) hummingbirds and (2) compare nesting success in these species with that of other temperate and tropical hummingbird species. With the exception of productivity values reported for Broad-tailed Hummingbirds (*Selasphorus platycercus*) by Waser and Inouye (1977) and Calder et al. (1983), the values presented in the present study are among the first reported for hummingbirds.

## STUDY AREAS

*Cliff.*—The area (elevation 1370 m) is near the town of Cliff along the east bank of the Gila River in Grant County, New Mexico (Fig. 1). It is approximately 990 m long and 42–104 m wide (9 ha), and is one of the longest continuous stands of woodland along the river. Numerous box-elder (*Acer negundo*), Goodding willow (*Salix gooddingii*), and Fremont cottonwood (*Populus fremontii*) trees characterize the upper story. The understory consists of woody and herbaceous species that include seepwillow (*Baccharis glutinosa*), skunk-bush (*Rhus trilobata*), chuchapate (*Ligusticum porteri*), buffaloweed (*Ambrosia trifida*), and various species of grass. Adjacent habitats include abandoned farm land, farmed land, and habitats similar to that of the study area.

*Rucker Canyon.*—The area (elevation 1870 m) is on the west side of the Chiricahua Mountains in Cochise County, Arizona (Fig. 1). It is confined primarily to an 800 × 75 m (5 ha) portion of the wooded creek bottom. Trees found within the area include several species of oak (*Quercus* spp.), alligator juniper (*Juniperus deppeana*), Arizona cypress (*Cupressus arizonica*), pines (*Pinus ponderosa* and *P. chihuahuana*), and Arizona sycamore (*Platanus wrightii*). The understory includes wild bean (*Phaseolus grayanus*), skunk-bush, and various species of grass. Adjacent hillsides are vegetated with oak and juniper interspersed with open areas containing numerous agaves (*Agave parryi*).

*Guadalupe Canyon.*—The area is along the United States-Mexico border in extreme southwestern New Mexico and extreme southeastern Arizona (Fig. 1). From its source in the Peloncillo Mountains of New Mexico, the canyon drains to the southwest, passing through Arizona before entering Mexico. Within Mexico the canyon joins the Río de San Bernardino, a tributary of the Río Yaqui. The area of study was confined primarily to the 150-m-wide canyon bottom that rises from the International Boundary northeastward into the New Mexico portion of the canyon, a distance of 8500 m (total area approximately 106 ha). The elevation of the canyon bottom ranges from 1305 m in the Arizona portion to 1366 m in the New Mexico segment.

Guadalupe Canyon is surrounded by Chihuahuan Desert scrub vegetation that interdigitates with the riparian vegetation of the creek bottom. On the basis of topography, exposure, and vegetation, I recognized three major habitats: riparian creek bottom, precipitous north-facing slopes, and xeric south-facing slopes. The creek bottom is characterized by numerous open areas interspersed with clumps of mature Arizona sycamores and Fremont cottonwoods, with understories of seepwillow and burro-brush (*Hymenoclea monogyra*) in central portions, and honey mesquite (*Prosopis glandulosa*), red barberry (*Berberis haematocarpa*), and netleaf hackberry (*Celtis reticulata*) near the edges. North-facing slopes generally rise abruptly from the canyon floor and are characterized by open areas interspersed with netleaf hackberry, one-seed juniper (*Juniperus monosperma*), oaks (*Quercus arizonica* and *Q. grisea*), soapberry (*Sapindus saponaria*), and agaves (*Agave schottii* and *A. parryi*), with dense shrub thickets composed of red barberry, honey mesquite, gray-thorn (*Condalia lyciodes*), woolly buckthorn (*Bumelia lanuginosa*), and poison ivy (*Rhus radicans*). Most south-facing slopes rise gradually from the canyon bottom and are characterized by open areas with scattered agaves and ocotillo (*Fouquieria splendens*) or thickets of mixed species that include honey mesquite, little-leaf sumac (*Rhus microphylla*), and white-thorn (*Acacia constricta*).

## METHODS

*Locating nests.*—The majority of nests were found by walking the length of each study area several times at the onset of each nesting period. Additional nests were found incidentally during the course of study and by deliberate search in segments where no nests had previously been found. Based on subsequent searches that occurred every 7–10 days through-

out the nesting season, and the relatively few additional nests that were discovered, I estimate that 90–95% of all hummingbird nests were found.

*Loss assessment.*—Over 85% (176 nests) of the 206 nests used in this analysis were found while they were under construction or were in the early stages of incubation. Several nests of each species in each study area were selected for intensive study (56 nests total); the status of all remaining nests was nonetheless checked at least once every 7–10 days. The status of some nests was obtained directly because eggs or young could be seen. For most nests, however, several factors were used to assess their status. The attentive patterns of females and their behavior at the nest proved to be the best indicators of status for those nests whose eggs or young could not be seen. Nests known to have been completed during the current season, but for which no behavioral data were available, were occasionally found. In these few instances (13.6% of all nests), one or more subtle cues such as the size and shape of the nest (see Calder 1973), the presence of excrement adhering to foliage adjacent to the nest (indicative of large young and successful fledging), or the presence of eggshell fragments (indicative of eggs and subsequent predation) were used to deduce the probable outcome.

*Data analysis and presentation.*—Comparisons designed to test whether nesting success varied seasonally (i.e., early vs late nests) for Black-chinned and Broad-billed hummingbirds in Guadalupe Canyon were made. Comparisons were based on the number of nests that succeeded and failed, and they were analyzed using a *G*-test, which was adjusted using Williams' correction factor (Sokal and Rohlf 1981:736). Comparisons over the 3-year period for both species were analyzed by combining probabilities from the former calculations (Sokal and Rohlf 1981:780) and by inverse interpolation (Rohlf and Sokal 1981:xii).

Nesting success and productivity were calculated using methods described by Ricklefs (1969, 1973) and Ricklefs and Bloom (1977). Annual production ($P$) of fledglings by a female was calculated using the equation $P = FB$, where $F$ is the expected rate at which young are fledged in a large population (young fledged/female × day) and $B$ is the length of the breeding season (days).

The rate at which young are fledged ($F$) was calculated by the expression $F = CSI$, where $C$ is clutch size, $S$ is breeding success (proportion of individuals that fledge), and $I$ is the rate of nest initiation (clutches/female × day). Rate of nest initiation was calculated by an equation that takes into account rate of nest failure and the interval between nestings, as follows (Ricklefs 1970):

$$I = \frac{m}{p_f + m(p_s r_s + p_f r_f)}$$

where $m$ is equal to nest mortality rate (proportion of nests failing per day), $p_s$ is the probability that a nest successfully fledges at least one young, $p_f$ is the probability of a nest failing before fledging young ($p_f = 1 - p_s$), $r_s$ is the delay before a new clutch is laid after successful fledging, and $r_f$ is the delay before a new clutch is laid after nest failure ($r_s$ and $r_f$ in the present study both = 10 days). Nesting success ($p_s$) is related to daily mortality rate ($m$) by the following expression:

$$p_s = e^{-mT}$$

where $e$ is the base of the logarithm and $T$ is equal to the length of the nest cycle from the initiation of nesting until fledging (days).

Breeding season length was calculated from the number of nests initiated each month by the following equation:

$$B = 30 \exp(-\sum p_i log_e p_i)$$

an index first used in the present context by MacArthur (1964). In this equation, $e$ is the

base of the natural logarithm and $p_i$ equals the proportion of clutches laid by a population during month $i$. This expression for breeding season takes into account the fact that breeding was not equally intense in all months during which eggs were found. The number of months of clutch initiation was multiplied by 30 to give the number of days ($B$) during which clutches were initiated.

## RESULTS

*Predation and other sources of nest mortality.*—I found predation to be the major cause of nest failure. Of the 206 nests analyzed, 129 (79.1%) failed prior to fledging young (Table 1). Predation was responsible for 102 of the failed nest attempts. Egg predation accounted for 72.5% of all predation losses. Predation on nestlings accounted for the remaining 27.5%. Failures resulting from other sources accounted for only 20.9% of all failed nest attempts.

Proportions of all losses in different study areas resulting from predation were similar: 70.6% at Cliff, where only Black-chinned Hummingbirds nested; 68.0% at Rucker Canyon, where Black-chinned and Magnificent hummingbirds nested; and 83.9% in Guadalupe Canyon, where Black-chinned, Broad-billed, Violet-crowned, and Costa's hummingbirds nested. Predation rates of Black-chinned nests were similar in all areas: 70.6% of all losses at Cliff, 70.8% at Rucker Canyon, and 82.3% in Guadalupe Canyon. Predation accounted for 75.0% of all Broad-billed losses, 100% of all losses for Costa's, and 85.7% of all losses for Violet-crowned hummingbirds.

Predation rates varied seasonally for Black-chinned Hummingbirds in Guadalupe Canyon. Nectar resource abundance in this area was decidedly bimodal (Fig. 2). Hummingbird nesting results for this area, which also showed some degree of bimodality (Fig. 2), were thus segregated into two periods based on the differential availability and dispersion of nectar (Baltosser 1983). The first period included those nests initiated prior to the sharp decline occurring on or about 17 June and those of the second period were begun after this date in 1976, 1977, and 1980. Predation accounted for 88.9%, 100%, and 100% of all Black-chinned losses during the first period, and for 90.9%, 64.3%, and 75.0% of all losses during the second period. Predation rates between periods were not compared for Broad-billed Hummingbirds because of small sample size. Comparisons of predation rates between periods for Costa's and Violet-crowned hummingbirds were not possible because each nested only during one of the two periods. Costa's Hummingbird nesting was completed each year prior to the beginning of the second nesting period (i.e., before 17 June), and Violet-crowned Hummingbird nesting did not begin until the second nesting period was under way (i.e., after 17 June).

The death of well-developed nestlings in three nests in Rucker Canyon

TABLE 1

SOURCES OF NEST MORTALITY FOR BLACK-CHINNED (BC), MAGNIFICENT (MA), BROAD-BILLED (BB), COSTA'S (CO), AND VIOLET-CROWNED (VC) HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

| Sources of nest mortality | Species and area | | | | | | |
|---|---|---|---|---|---|---|---|
| | BC[a] | BC[b] | MA[b] | BC[c] | BB[c] | CO[c] | VC[c] |
| Number of nests: | | | | | | | |
| Abandoned before eggs | 3 (12)[d] | 2 (7) | 1 (50) | 7 (7) | 1 (5) | 0 | 0 |
| Egg mortality | | | | | | | |
| Egg predation | 9 (35) | 14 (47) | 0 | 32 (32) | 5 (25) | 9 (82) | 5 (31) |
| Structural failure | 0 | 1 (3) | 0 | 1 (1) | 0 | 0 | 0 |
| Eggs unhatched | 0 | 0 | 0 | 1 (1) | 1 (5) | 0 | 0 |
| Human intervention | 0 | 1 (3) | 0 | 0 | 0 | 0 | 0 |
| Nestling mortality | | | | | | | |
| Nestling predation | 3 (12) | 3 (10) | 0 | 19 (19) | 1 (5) | 1 (9) | 1 (6) |
| Structural failure | 0 | 0 | 0 | 1 (1) | 0 | 0 | 0 |
| Nestlings dead in nest | 2 (8) | 3 (10) | 0 | 1 (1) | 0 | 0 | 1 (6) |

[a] Cliff study area.
[b] Rucker Canyon study area.
[c] Guadalupe Canyon study area.
[d] (Percent of all nests.)

in 1977 is believed to have resulted from inclement weather. During the 46-day period from 6 July through 20 August 1977, the study area received 22.3 cm of rain, which fell on 22 days. Only 6.93 cm of rain fell during the same period in 1976, and it rained on only 11 days. The presence of dead young that would have soon fledged in nests at Cliff may have also resulted from rainy weather, rather than from abandonment or mortality of the female. Indeed, a female at one of the two nests that contained dead nestlings built a second nest and initiated a new clutch on top of a large dead nestling that was sealed into the lower nest.

Daily mortality rates, which encompass all forms of nest failure, for all three areas and species nesting within these areas were just over 2.0% ($\bar{x}$ = 2.28 ± 1.22% [SD]) of all nests in each population. Daily losses averaged 2.52 ± 0.15% of all hummingbird nests at Cliff, 3.10 ± 1.56% of all nests at Rucker Canyon, and 1.99 ± 1.20% of all nests in Guadalupe Canyon. Pooled Black-chinned losses from each study area averaged 3.01 ± 1.01% per day, while those of Broad-billed and Violet-crowned hummingbirds averaged 1.22 ± 0.86% and 1.36 ± 0.25%, respectively. Daily mortality, based on limited sample size, was 3.94% for Costa's Hummingbirds and 1.39% for Magnificent Hummingbirds.

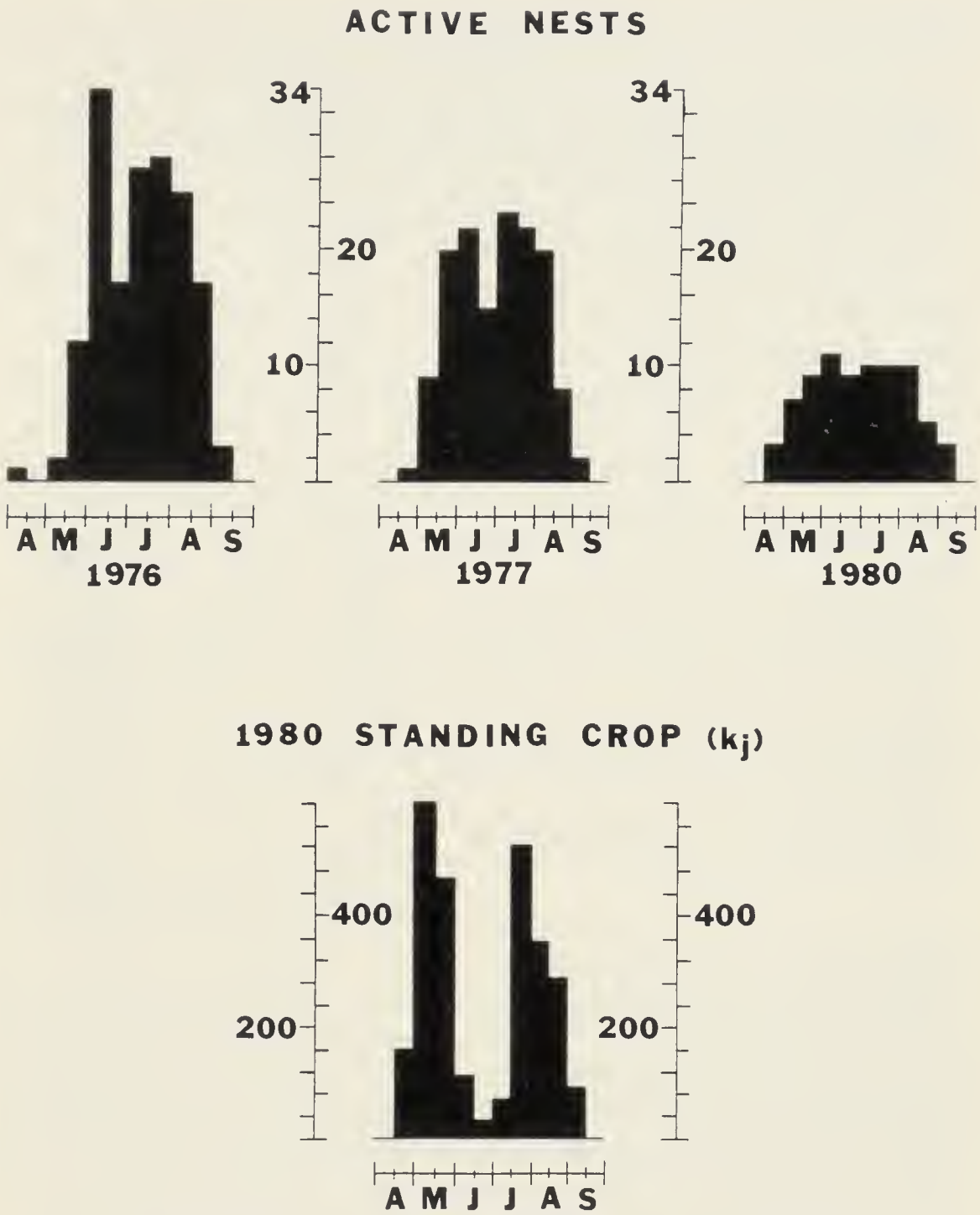


FIG. 2. Nesting phenology and abundance of active nests of hummingbird species in Guadalupe Canyon in relation to 1980 standing crop nectar values. (In 1976 and 1977 standing crops appeared to be similar to those of 1980, but only qualitative [i.e., abundance recorded as rare, common, or abundant] measurements were made.)

TABLE 2

YEARLY NESTING SUMMARY SHOWING THE TOTAL NUMBER OF BLACK-CHINNED, MAGNIFICENT, BROAD-BILLED, COSTA'S, AND VIOLET-CROWNED HUMMINGBIRD NESTS; THE NUMBER OF NESTS THAT PRODUCED FLEDGED YOUNG; AND THE PERCENT FLEDGING SUCCESS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

| Species | Area | Year | No. nests | No. fledged (% fledging success) |
|---|---|---|---|---|
| Black-chinned | Cliff | 1976 | 15 | 5 (33.3) |
| | | 1977 | 11 | 4 (36.4) |
| Black-chinned | Rucker Canyon | 1976 | 17 | 4 (23.5) |
| | | 1977 | 13 | 2 (15.4) |
| Magnificent | Rucker Canyon | 1976 | 2 | 1 (50.0) |
| | | 1977 | 0 | 0 |
| Black-chinned | Guadalupe Canyon | 1976 | 46 | 20 (43.5) |
| | | 1977 | 38 | 16 (42.1) |
| | | 1980 | 17 | 3 (17.7) |
| Broad-billed | Guadalupe Canyon | 1976 | 10 | 6 (60.0) |
| | | 1977 | 5 | 4 (80.0) |
| | | 1980 | 5 | 2 (40.0) |
| Costa's | Guadalupe Canyon | 1976 | 4 | 0 |
| | | 1977 | 6 | 1 (16.7) |
| | | 1980 | 1 | 0 |
| Violet-crowned | Guadalupe Canyon | 1976 | 5 | 3 (60.0) |
| | | 1977 | 6 | 3 (50.0) |
| | | 1980 | 5 | 3 (60.0) |

*Fledging success.*—I have defined fledging success as the proportion of nests, including those abandoned before eggs were laid, in which at least one young fledged. Average success for all species, areas, and years was 37.0 ± 22.4% (Table 2). Success at Cliff was 34.8 ± 2.1%, at Rucker Canyon 29.6 ± 18.1%, and at Guadalupe Canyon 39.2 ± 25.5%.

Black-chinned Hummingbird nesting success averaged 19.5 ± 5.8% in Rucker Canyon and 34.5 ± 14.5% in Guadalupe Canyon. Average success of Broad-billed Hummingbirds was 60.0 ± 20.0%, that of Costa's 5.6 ± 9.6%, and that of Violet-crowned Hummingbirds 56.7 ± 5.8%.

Incubation success for Black-chinned Hummingbirds between the first and second nesting periods (Table 3) was not significantly different in 1976 ($G_{adj}$ = 0.80, df = 1, $P$ = 0.44) or 1977 ($G_{adj}$ = 2.90, df = 1, $P$ = 0.09). In the 1980 season, however, success during incubation was significantly greater in the second nesting period ($G_{adj}$ = 5.56, df = 1, $P$ =

0.02). Incubation success for the cumulative three years between periods for this species was also significantly greater during the second nesting period ($G_{adj}$ = 14.24, df = 6, $P$ = 0.03).

Black-chinned success during the nestling phase did not differ significantly between periods except for 1977, although in 1980 the difference approached significance ($G_{adj}$ = 2.96, df = 1, $P$ = 0.09). Nestling success in 1977 was significantly greater during the first nesting period ($G_{adj}$ = 6.08, df = 1, $P$ = 0.02).

Because greater incubation success during second nesting periods tended to be canceled by greater nestling success during first periods, overall success between periods for the duration of nesting did not differ significantly for Black-chinned Hummingbirds. Nesting success between periods, based on combined probabilities for all three years, also was not significantly different ($G_{adj}$ = 2.78, df = 6, $P$ = 0.83).

Broad-billed Hummingbird incubation success between periods followed a pattern similar to that of Black-chinned Hummingbirds (Table 3). Success was greater during the second period except for 1977, but the seasonal differences were not significant. Only during 1980 did any of the values approach a level of significance ($G_{adj}$ = 2.18, df = 1, $P$ = 0.19).

Broad-billed Hummingbirds were highly successful during the nestling phase, and only in 1980 did failures occur. Success for the duration of nesting between periods for Broad-bills was similar to that of Black-chins. Success was greater during the second period in 1976 and 1980 than in the first nesting period. Success in 1977 was, however, greater the first period than during the second period.

Comparisons of nesting success between periods within a given year for Costa's and Violet-crowned hummingbirds were not made because each nested only during one of the two periods (Table 3). Between-year comparisons of the same nesting periods for Costa's, however, did reveal some interesting trends. Nineteen seventy-seven was the only year the species had any success. Broad-billed success was greater during the first period in 1977, the only year in which that was the case. Nesting success of Violet-crowned Hummingbirds was similar between years.

*Productivity.*—Hummingbird productivity (number of young fledged per female), based on pooled data for each species, area, and year, was 1.23 ± 0.86 young per female (Table 4). The average number of young produced per female was 0.80 ± 0.42 at the Cliff study area, 0.74 ± 0.37 at Rucker Canyon, and 1.43 ± 0.94 at Guadalupe Canyon.

Black-chinned Hummingbird productivity in Guadalupe Canyon averaged 1.82 ± 0.99, as compared to 0.80 ± 0.05 and 0.53 ± 0.05 for the species at Cliff and Rucker Canyon, respectively. On a daily basis, Black-

TABLE 3

GUADALUPE CANYON HUMMINGBIRD NESTING SUMMARY FOR 1976, 1977, AND 1980 SHOWING THE PERCENT SURVIVAL OF NESTS (NESTING SUCCESS) FOR EACH SPECIES, STAGE, AND PERIOD OF THE NESTING CYCLE

| Species and stage of nesting | 1976 | | 1977 | | 1980 | | All years | |
|---|---|---|---|---|---|---|---|---|
| | First nesting | Second nesting | First nesting | Second nesting | First nesting | Second nesting | First nesting | Second nesting |
| Black-chinned | | | | | | | | |
| Incubation | 68.0 | 80.0 | 42.9 | 70.6 | 16.7 | 80.0 | 48.3 | 76.2 |
| Nestling | 52.9 | 68.8 | 100 | 58.3 | 100 | 25.0 | 71.4 | 59.4 |
| Overall | 36.0 | 55.0 | 42.9 | 41.2 | 16.7 | 20.0 | 34.5 | 45.2 |
| Broad-billed | | | | | | | | |
| Incubation | 50.0 | 71.4 | 100 | 66.7 | 33.3 | 100 | 57.1 | 75.0 |
| Nestling | 100 | 100 | 100 | 100 | 100 | 50.0 | 100 | 88.9 |
| Overall | 50.0 | 71.4 | 100 | 66.7 | 33.3 | 50.0 | 57.1 | 66.7 |
| Costa's | | | | | | | | |
| Incubation | 0 | | 33.3 | | 0 | | 18.2 | |
| Nestling | 0 | | 50.0 | | 0 | | 50.0 | |
| Overall | 0 | | 16.7 | | 0 | | 9.1 | |
| Violet-crowned | | | | | | | | |
| Incubation | | 80.0 | | 66.7 | | 60.0 | | 68.8 |
| Nestling | | 75.0 | | 75.0 | | 100 | | 81.8 |
| Overall | | 60.0 | | 50.0 | | 60.0 | | 56.3 |

chinned Hummingbird productivity was 0.018 young per female in Guadalupe Canyon, 0.010 in Rucker Canyon, and 0.017 at Cliff.

Average productivity was 2.32 ± 0.08 for Broad-billed Hummingbirds and 1.43 ± 0.02 for Violet-crowned Hummingbirds. Costa's Hummingbirds rarely fledged young in Guadalupe Canyon, where their productivity was 0.16 ± 0.27. The productivity of Magnificent Hummingbirds at Rucker Canyon was 1.16 young per female. Daily productivity was virtually identical for Broad-billed (0.028 young/female) and Violet-crowned (0.027 young/female) hummingbirds, and greater than Costa's (0.003 young/female) and Magnificent (0.019 young/female) hummingbirds.

## DISCUSSION

*Sources of mortality.*—Predation was the major cause of hummingbird nest failure in each of the three study areas. In other species of birds, mortality rates resulting from predation vary, but are frequently as low as ½%/day of all nests in a population in many large raptorial and oceanic species, and as high as 5%/day in some small land birds and precocial

TABLE 4

COMPONENTS OF BREEDING PRODUCTIVITY SHOWING THE NUMBER OF YOUNG FLEDGED PER FEMALE PER YEAR FOR BLACK-CHINNED, MAGNIFICENT, BROAD-BILLED, COSTA'S, AND VIOLET-CROWNED HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA

| Species | Area | Year | Season length (months)[a] | Clutch size (eggs) | Nest mortality[b] | Nest period (days) | Nesting success[c] | Young/female |
|---|---|---|---|---|---|---|---|---|
| Black-chinned | Cliff | 1976 | 1.10 | 2 | 0.0262 | 42 | 0.3333 | 0.50 |
| | | 1977 | 1.99 | 2 | 0.0241 | 42 | 0.3636 | 1.10 |
| Black-chinned | Rucker Canyon | 1976 | 1.60 | 2 | 0.0344 | 42 | 0.2353 | 0.56 |
| | | 1977 | 1.97 | 2 | 0.0446 | 42 | 0.1538 | 0.49 |
| Magnificent | Rucker Canyon | 1976 | 2.00 | 2 | 0.0139 | 50 | 0.5000 | 1.16 |
| | | 1977 | 0 | 0 | 0 | 0 | 0 | 0 |
| Black-chinned | Guadalupe Canyon | 1976 | 3.23 | 2 | 0.0195 | 42 | 0.4400 | 2.11 |
| | | 1977 | 4.09 | 2 | 0.0206 | 42 | 0.4210 | 2.63 |
| | | 1980 | 3.44 | 2 | 0.0414 | 42 | 0.1760 | 0.72 |
| Broad-billed | Guadalupe Canyon | 1976 | 2.56 | 2 | 0.0096 | 42 | 0.6670 | 2.40 |
| | | 1977 | 1.99 | 2 | 0.0053 | 42 | 0.8000 | 2.24 |
| | | 1980 | 3.78 | 2 | 0.0218 | 42 | 0.4000 | 2.32 |
| Costa's | Guadalupe Canyon | 1976 | 1.75 | 2 | 0 | 45 | 0 | 0 |
| | | 1977 | 1.89 | 2 | 0.0394 | 45 | 0.1667 | 0.47 |
| | | 1980 | 1.00 | 2 | 0 | 45 | 0 | 0 |
| Violet-crowned | Guadalupe Canyon | 1976 | 1.65 | 2 | 0.0122 | 42 | 0.6000 | 1.44 |
| | | 1977 | 1.96 | 2 | 0.0165 | 42 | 0.5000 | 1.40 |
| | | 1980 | 1.65 | 2 | 0.0122 | 42 | 0.6000 | 1.44 |

[a] Number of months during which eggs were present.
[b] Proportion of nests in the population that failed each day.
[c] Proportion of nests that fledged at least one young.

species (Ricklefs 1969). Daily losses in my study averaged just over 2%. Failures resulting from other sources such as abandonment, structural failure, and infertility were of less importance and were similar to those found in other studies (see Ricklefs 1969).

I believe the majority of Black-chinned and Violet-crowned losses to predation in Guadalupe Canyon resulted from avian predators. This conclusion is based in part on the fact that I witnessed the loss of one Black-chinned nest to predation by Gray-breasted Jays (*Aphelocoma ultramarina*), on the frequent mobbing of Hooded Orioles (*Icterus cucullatus*) and Summer Tanagers (*Piranga rubra*), and on the fact that there was a significant inverse relationship ($r = -0.65$, df = 11, $P < 0.05$) between nest height and nesting success for Black-chinned Hummingbirds (Baltosser 1983). Similarly, higher and more-exposed nests of Violet-crowned Hummingbirds, which were in microhabitats similar to Black-chinned Hummingbird nests (Baltosser 1983), also suffered greater predation.

Broad-billed Hummingbird losses to predation are thought to have resulted primarily from snake predation. Nests of this species were very close to the ground ($\bar{x} = 1.1 \pm 0.5$ m), which placed them out of the path of most avian predators. The maximum diameter of limbs to which the pendent nests were attached was usually <1 cm, and predators other than snakes would have had difficulty extracting the contents without damaging the nest. With the exception of one nest that had a medium-sized hole similar to one a snake might produce when forcing eggs into its mouth, nests lost to predation were not altered and there were no eggshell fragments, which are often found in nests lost to avian predation.

Few data pertaining to possible sources of predation on Costa's Hummingbird nests were obtained because most nests were lost to predation very early in the nesting cycle. Few data that would indicate the source of predation on Black-chinned nests in Rucker Canyon and Cliff were obtained. Nests that failed were in some cases completely destroyed, while others were not appreciably altered.

*Nesting success and hummingbird productivity.*—Nesting success for hummingbird species in the present study, omitting Magnificent Hummingbirds because of extremely low sample size, was similar to that reported for other temperate and tropical hummingbirds (Woods 1927; Skutch 1931, 1940, 1966; Legg and Pitelka 1956; Stiles 1973; Carpenter 1976; Waser and Inouye 1977; Calder et al. 1983). Hummingbird nesting success in the above studies, based on 11 species and only those nests that contained eggs (i.e., nests abandoned before eggs were laid were not included) ranged from 20% to 89%. Average nesting success in the present study (deleting those nests abandoned before eggs were laid) ranged from

9% to 62%. Black-chinned nesting success for all three study areas was 34.0 ± 11.0%, which is similar to the 31.9 ± 1.4% reported for this species by Stiles (1973). Black-chinned success may therefore be relatively constant throughout the range of the species.

Nesting survivorship for all hummingbirds in each of the three study areas was generally higher during the nestling stage than during the incubation stage. This is consistent with other studies (see Best and Stauffer 1980) and probably stems in part from the fact that certain mortality factors, such as nest desertion, occur more frequently before hatching. In addition, especially vulnerable nests are more likely to be found and destroyed by predators early in the nesting cycle (e.g., Nolan 1978).

Ricklefs (1969) has suggested that in simpler habitats, or those with low productivity (i.e., arid and arctic), uncommon species tend to have relatively high nesting success as compared to more common species with similar nesting requirements. Reasons why rarer species like the Violet-crowned Hummingbird would experience greater success (56.7%) than more common species such as the Black-chinned Hummingbird (34.5%) were not given. During 1980, however, foliage in Guadalupe Canyon had been reduced by 75% as the result of an extremely severe freeze, and thus very little vegetative cover was available for nesting. Rarer and dominant Violet-crowned Hummingbirds nonetheless nested in virtually the same sites as in previous years, which were affected less by the freeze than sites available to Black-chinned Hummingbirds. The fewer Black-chinned Hummingbirds nesting in 1980 and their reduced nesting success in that year may have resulted in part from the effects of the freeze on vegetation. In contrast, in 1976 and 1977, poorer nesting success by Black-chinned Hummingbirds appeared to have been related to the amount of interference experienced by nesting female hummingbirds and subsequent predation resulting from the commotion and betrayal of the nest site (see Skutch 1949). In 1976, for example, there was a significant inverse correlation ($r = -0.99$, df = 1, $P < 0.05$) based on 6663 minutes of intensive observation at 36 nests, between the number of times female Black-chinned, Broad-billed, and Violet-crowned Hummingbirds were disturbed or induced to leave their nests and their nesting success (Baltosser 1983). Similar interactions were frequently observed in 1977, but they were not quantified.

The exceptionally high nesting success (89%) of the Andean Hillstar (*Oreotrochilus estella*) reported by Carpenter (1976) is most likely related to the fact that it nests in enclosed and inaccessible rocky areas, including caves. Similarly, the greater nesting success of Broad-billed Hummingbirds (62%) in the present study was probably due in part to the protection

provided by their nest sites. Nests of this species were invariably next to rock outcrops or in extremely dense thickets, which provided a great deal of protection and seclusion.

In addition to predation, nesting success for Black-chinned Hummingbirds in Rucker Canyon and Cliff appeared to be affected by inclement weather. The death of well-developed nestlings in nests at Rucker Canyon and Cliff perhaps resulted from the dampness and cooler temperatures associated with extended periods of rainy weather.

Recently, Miller and Gass (1985) examined the available predation data on foraging adult hummingbirds in temperate habitats. They concluded that there is no indication that predation is a significant risk factor to adults. Much of my research (Baltosser 1978, 1983) supports their conclusions for foraging adults, but the results of the present study indicate that predation is an important mortality factor for hummingbird eggs and nestlings.

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# THE HISTORY OF THE SOUTHERN FLORIDA WOOD STORK POPULATION

James A. Kushlan and Paula C. Frohring[1]

Abstract.—The largest segment of the North American Wood Stork (*Mycteria americana*) population traditionally nested in southern Florida, where its perceived population decrease over the last 50 years resulted in its addition to the Federal endangered species list. Previously published reports placed the southern Florida population at 30,000 to 100,000 storks. A complete search of published and unpublished records of Wood Storks nesting in southern Florida, however, failed to support such a long-term population decrease. We cannot demonstrate that the historical population was any larger than it was in 1967, when there were 9400 pairs. The Corkscrew-Big Cypress nesting group, not that of the Everglades, was historically the most numerically important population segment. The historic nesting location for southernmost Wood Storks was not inland in the Everglades but on Cape Sable, which has been subject to the effects of drainage canals. The population size of several decades ago is irrelevant to current conservation strategy because the southern Florida marshes have been irrevocably altered reducing their ability to support storks. We can document a population decrease of 75% from 1967 to 1981–82 in southern Florida, a time frame coincident with the operation of water management policies in the Everglades. Wood Storks recently have begun abandoning traditional colony sites in Everglades National Park in favor of sites in shallow reservoirs to the north. Drainage of the Big Cypress Swamp and maintenance of seasonally excessive water levels in the Everglades of Everglades National Park account for the stork's repeated nesting failure and population decrease. Water levels can be manipulated in the Everglades to enhance nesting success and assist in population stabilization. *Received 5 Aug. 1985, accepted 1 Feb. 1986.*

The population stability of the Wood Stork (*Mycteria americana*) in North America long has been a matter of concern and comment. Reproductive failures and apparent population decreases have been well publicized for decades (e.g., Sprunt and Kahl 1960, Allen 1964), and have resulted in the recent addition of this population to the United States Federal list of endangered species (USFWS 1984). Although the North American nesting range of the species includes most of the Gulf and Atlantic coastal plain, the largest population segment traditionally nested in southern Florida. It is the decrease of this population that has created the perception of instability for the North American population as a whole. Thus the history of southern Florida Wood Storks is of overriding importance in evaluating the trend of the U.S. population.

The decreasing status of North American and southern Florida Wood Storks has been described repeatedly (Allen 1958, 1964; Allen et al. 1958; Sprunt and Kahl 1960; Kahl 1964; Robertson and Kushlan 1974; Kushlan

[1] Dept. Biological Sciences, East Texas State Univ., Commerce, Texas 75428.

and White 1977; Ogden 1978a; Ogden and Nesbitt 1979; Ogden and Patty 1981). Unfortunately, these descriptions are not based on explicit evaluations of the primary historic record. Indeed, a variety of estimates for the historic population size exists, and these have been made over various geographical areas. For example Allen estimated that U.S. breeding population was 150,000 in the 1930s (Palmer 1962). He later decreased this estimate to "well over 100,000" (Allen 1964). Ogden (1978b) implicitly questioned Allen's record and concluded that "there may have been 60,000 total storks in the U.S. population at about 1930," including 30,000 breeding adults in southern Florida (Ogden and Patty 1981). Ogden's stated concerns over crucial early records have not precipitated any uniformity of opinion with respect to historic population size, even within the U.S. Fish and Wildlife Service. Its recent estimates include "20,000 pairs [40,000 birds] in the 1930's" (USFWS 1984) and "an estimated southeastern U.S. nesting population of 75,000 to 100,000 pairs in the early 1900's" (Parker 1985).

Clearly divergent conclusions demand a critical assessment of the primary data base. In this paper we document the history of the Wood Stork population segment in southern Florida, based on an objective evaluation of specific historic records and on comprehensive censuses that we conducted during 1974–82. We confirm Ogden's (1978b) concern that early records were exaggerated, argue for the rejection of those records, and provide the documentable history of the Wood Stork's status in southern Florida.

## METHODS

We assembled and reviewed all available historic and recent information on the southern Florida Wood Stork population. This review included searches of six computerized and one noncomputerized bibliographic sources, complete runs of 35 technical and conservation periodicals, the Colonial Bird Register (Cornell Laboratory of Ornithology), the egg collections at North American museums (J. A. Rodgers, pers. comm.), and, especially, unpublished material at Everglades National Park, the National Audubon Society, and U.S. Fish and Wildlife Service Wildlife Refuges. This material included field notes, reports of censuses and surveys, observation files, and other notes, reports, and memorabilia.

Recent estimates (1974–1982) in the Everglades were derived from our consistent monthly aerial censuses covering all possible nesting habitat in and near the Everglades. Censuses were conducted carefully to provide complete coverage and acceptably unbiased estimates of the number of birds in colony sites. Censuses of colonies in the northern Big Cypress Swamp were sponsored by the National Audubon Society (Kahl 1964; J. Cutlip, pers. comm.; Ogden and Patty 1981).

This search resulted in over 900 unique records of Wood Stork occurrences at colony sites, from 1880 through 1982. Data-base manipulations were performed on a UNIVAC 1100 computer at the Southeast Regional Data Center, Florida International University, Miami, Florida.

Our goal was to elucidate the trend in the nesting population. It is not possible to evaluate

total population size in that the only census data available are the number of birds seen and counted at colony sites. Acceptability of a record of nesting was based upon three criteria: (1) a definite statement that nesting occurred; (2) a definite statement of the number of pairs, nests, or birds; and (3) the credibility of the source. We do not discuss reports in the text that fail to meet these criteria, except for a few frequently cited examples central to previous misunderstandings of the Wood Stork's history.

## RESULTS

*Colony sites.*—We identified 51 distinct colony sites used by nesting Wood Storks in southern Florida. We do not evaluate the history on the basis of colony sites, however, because such an approach is misleading. Many colony sites are inadequately documented, and all are transitory. Furthermore, colony sites are not a natural division of a population, as there is no indication that storks are attached to a single site. The traditional emphasis on colony sites inhibits an understanding of more important regional patterns. Therefore we have grouped colony sites used in southern Florida into seven regions based upon geography, foraging sites, and habitat (Fig. 1). We do not assume storks are faithful to these regions and in fact demonstrate population shifts among them.

The northern Big Cypress colonies are in Region VII. We divided the more southern colonies, Kahl's (1964) Everglades-mangrove group, into six regions (I–VI). Region I is the area of Cape Sable along the southwestern Florida coast, including the following named colony sites: Bear Lake, Alligator Lake, Flinthead, North Coot Bay, Mud Lake, Durden Key, Cattail Lake, and North Fox Lakes. Region II is the Hells Bay area inland of the southcentral Florida coast, including the following named colony sites: Old Lane River, East River, Ironhead Rookery, Lane River, Noname Rookery, Cuthbert Lake, and North Cuthbert Lake. Region III is the southeastern Florida Coast, including the following named colony sites: Joe Bay, Eagle Key, Glades Canal, and Madeira. Region IV is the southern Everglades including named colony sites at Shark River, Quok Creek, Mudhole, P-36, and North Broad River. Region V is the northern Everglades including 13 sites, most unnamed or inconsistently named, among which storks have moved frequently. Region VI is the southern Big Cypress Swamp including the following named sites: 40-Mile Bend, Loop Road, Monroe Station, and Jetport. Region VII covers Corkscrew Swamp and the northern Big Cypress Swamp area including the following named sites: Deep Lake, Corkscrew Swamp, Okalacoochee, Immokalee Road, Fahkahatchee, Bear Island, Doctor's Hammock, Sadie Cypress, Rocky Lake, and at least one unnamed site.

*Historic population estimates.*—We have documented storks nesting in southern Florida in 72 of 102 years, from 1880 through 1982 (Table 1). Because no information exists for many early years, it may be more useful

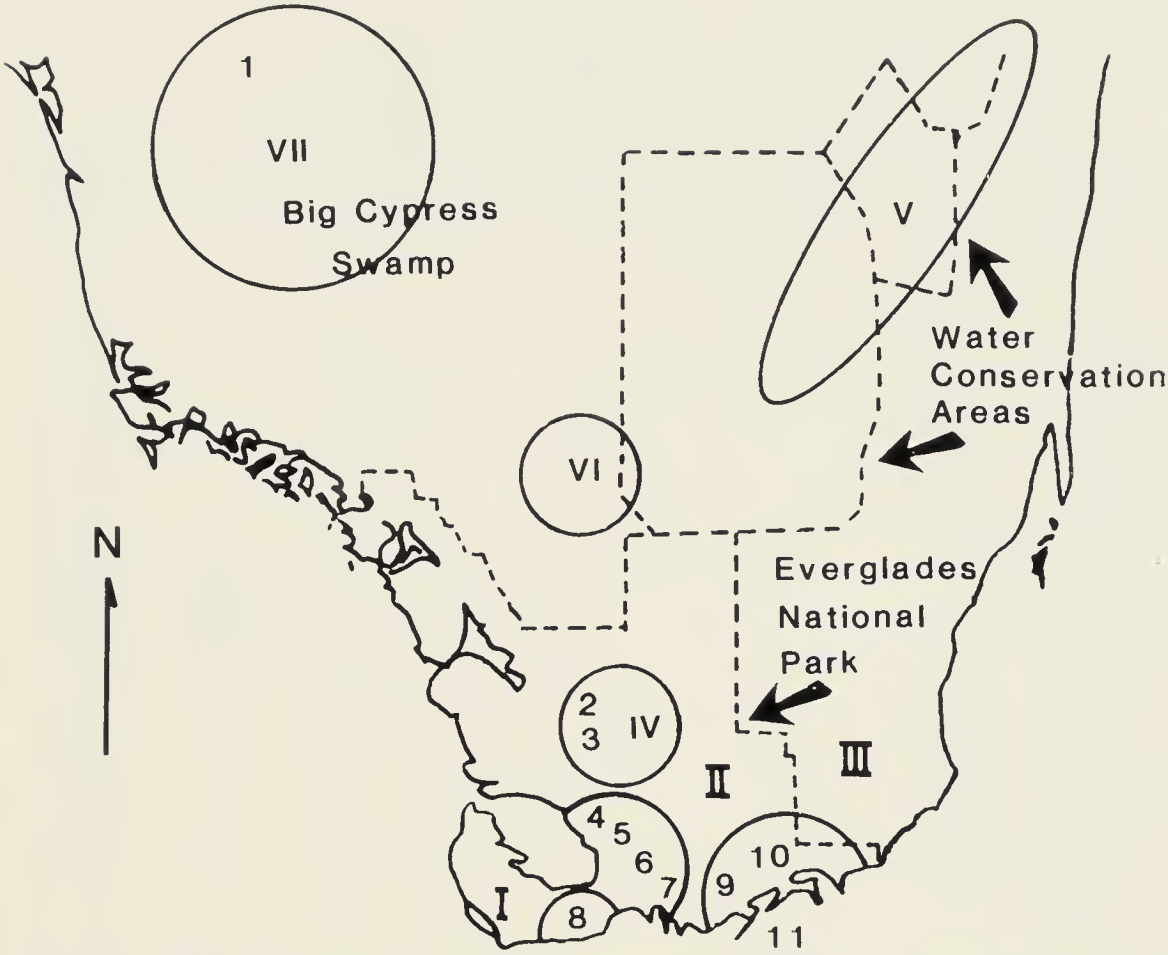


FIG. 1. Map of southern Florida showing seven Wood Stork nesting regions: (I) Cape Sable, (II) Hells Bay, (III) Southeastern Florida coast, (IV) Southern Everglades, (V) Northern Everglades, (VI) Southern Big Cypress Swamp, and (VII) Corkscrew Swamp and northern Big Cypress Swamp. Colony sites discussed in the text are located by number: (1) Corkscrew Swamp, (2) Rookery Branch, (3) Quok Creek, (4) Old Lane River, (5) Lane River, (6) East River, (7) Alligator Lake, (8) Cuthbert, (9) Madeira, (10) Joe Bay, and (11) Eagle Key. Other colony sites in each region are listed in the text.

to note that there is documentation for Wood Storks nesting in southern Florida every year for 60 years, beginning in 1923.

In the vast majority of cases, we know only that nesting occurred. Relatively few records included information on the number of pairs or nests. In some cases, certain numbers of birds were noted as being near a known nest site, but this information was inadequate to infer a number of nesting pairs. It is not possible to know how many storks occurred in southern Florida in the 1800s. Acceptable estimates of nesting numbers for the early 1900s were available only from the Corkscrew-northern Big Cypress Region. Numbers in other regions are unavailable before the early 1950s.

The earliest nesting in southern Florida was documented from the Cape

TABLE 1

HISTORICAL NUMBERS OF WOOD STORKS NESTING IN SOUTHERN FLORIDA

| Year | Maximum number of pairs (nests) by region[a] | | | | | | | Southern Florida total |
|---|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | VI | VII | |
| 1880 | +[b] | | | | | | | + |
| 1883 | + | | | | | | | + |
| 1888 | + | | | | | | | + |
| 1891 | + | | | | | | | + |
| 1892 | + | | | | | | + | + |
| 1895 | + | | | | | | + | + |
| 1901 | + | | | | | | | + |
| 1903 | 20 | | | | | | | 20 |
| 1910 | + | | | | | | | + |
| 1911 | | | | | | | 500 | 500 |
| 1912 | | | | | | | 8000 | 8000 |
| 1913 | | | | | | | 5000 | 5000 |
| 1915 | + | | | | | | | + |
| 1923 | + | | | | | | | + |
| 1924 | 230 | | | | | | | 230 |
| 1925 | + | | | | | | | + |
| 1926 | + | | | | | | + | + |
| 1927 | 300 | | | | | | | 300 |
| 1928 | + | | | | | | | + |
| 1929 | + | | | | | | | + |
| 1930 | | | | + | | + | | + |
| 1932 | + | + | | | | + | + | + |
| 1933 | + | + | | + | | | | + |
| 1934 | 500 | + | | | | | | 500 |
| 1935 | | | | + | | | + | + |
| 1936 | + | | | | | | | + |
| 1937 | + | | | | | | | + |
| 1938 | 86 | + | | | | | | 86 |
| 1939 | | | | | | | + | + |
| 1940 | + | + | | | | | | + |
| 1941 | + | | | | | | | + |
| 1942 | | + | | | | | | + |
| 1943 | | 300 | | | | | | 300 |
| 1944 | + | + | | | | | | + |
| 1945 | | + | | | | | | + |
| 1946 | | + | | + | | | | + |
| 1947 | | + | | | | | | + |
| 1948 | | + | + | | | | | + |
| 1949 | | + | + | | | | | + |
| 1950 | | 3525 | + | + | | | + | 3525 |
| 1951 | | + | + | | | | | + |
| 1952 | | 250 | | + | | | + | 250 |
| 1953 | | + | | | | | | + |

TABLE 1
CONTINUED

| Year | Maximum number of pairs (nests) by region[a] | | | | | | | Southern Florida total |
|---|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | VI | VII | |
| 1954 | | + | | | | | | + |
| 1955 | | + | | | | | + | + |
| 1956 | | + | | | | | + | + |
| 1957 | | + | | | | | 0 | + |
| 1958 | | 580 | 5 | 25 | | 25 | 1615 | 2250 |
| 1959 | | 1450 | | | | | 4655 | 6105 |
| 1960 | | 1900 | | | | | 6635 | 8535 |
| 1961 | | + | + | | | | 6000 | 6000 |
| 1962 | | 150 | 0 | 0 | | | 0 | 150 |
| 1963 | | 1200 | 300 | 100 | | | 3000 | 4600 |
| 1964 | | + | | | | | 0 | + |
| 1965 | 0 | 1000 | 500 | 150 | | | | 1650 |
| 1966 | 0 | 850 | 750 | 0 | | | 3000 | 4600 |
| 1967 | 800 | 825 | 500 | + | | | 7300 | 9425 |
| 1968 | 0 | 437 | 590 | 0 | | | 5000 | 6027 |
| 1969 | 0 | 88 | 190 | 0 | | | 3500 | 3778 |
| 1970 | 0 | 19 | 150 | 0 | | | 1900 | 2069 |
| 1971 | 0 | 258 | 0 | 200 | | | 3000 | 3458 |
| 1972 | 0 | 58 | 275 | 0 | | | 1500 | 1833 |
| 1973 | 0 | 388 | 500 | 0 | | | 0 | 888 |
| 1974 | 0 | 700 | 250 | 0 | 0 | 0 | 1900 | 2850 |
| 1975 | 0 | 810 | 125 | 0 | 0 | 0 | 3000 | 3935 |
| 1976 | 0 | 1275 | 35 | 0 | 0 | 0 | 2300 | 3610 |
| 1977 | 0 | 635 | 80 | 0 | 0 | 0 | 200 | 915 |
| 1978 | 0 | 16 | 3 | 0 | 0 | 0 | + | 19 |
| 1979 | 0 | 1075 | 275 | 0 | 0 | 15 | 900 | 2265 |
| 1980 | 0 | 80 | 1 | 0 | 0 | 0 | 1175 | 1256 |
| 1981 | 0 | 381 | 0 | 0 | 297 | 0 | 1500 | 2178 |
| 1982 | 0 | 670 | 0 | 0 | 549 | 0 | 18 | 1237 |

[a] I = Cape Sable; II = Hells Bay; III = southeastern coast; IV = southern Everglades; V = northern Everglades; VI = southern Big Cypress Swamp; VII = Corkscrew Swamp-northern Big Cypress Swamp. See Fig. 1 for locations of regions.
[b] + indicates that nesting was reported but that numbers either were not given or are not reliable.

Sable Region (Region I) in the late 1800s (Table 1). This information comes from the activities of naturalists and egg collectors in the latter decades of the nineteenth century. Storks nested on Cape Sable through the 1930s and in much reduced frequency into the 1940s. Unfortunately, the numbers of nests were not specifically documented for most of this period. In 1926, 1500 Wood Storks were reported "with their nests and eggs and young" (Townsend 1926); in 1937, 2500 birds were reported and four colony sites were used. Thus it would seem that the number of

birds using Cape Sable was in the low thousands and that the numbers nesting were no higher and probably were lower. Holt and Sutton (1926) reported 230 nests in 1924 and Christy (1928) reported 300 pairs in 1927 at the Alligator Lake Site. This colony was frequently visited and reported on, as for example by Sutton (1923) in 1923, Holt (1929) in 1924, and Howell (1941) in the 1934 nesting season. Storks abandoned nesting sites on Cape Sable after the 1936 hurricane.

Region II, encompassing Hells Bay, includes several famous colony sites such as Cuthbert and East River. The Cuthbert site holds an important place in North American conservation history. The colony site was discovered by hunters at least as early as 1890 (Moore 1953) and was popularized through the visits of Bent, Job, and Chapman early in the century (Bent 1904, 1926; Dutcher 1904; Job 1905; Chapman 1908), and by the murder of bird warden Guy Bradley in 1904, who was guarding it. (See a later photograph of the colony site in Allen, 1964.) During none of these visits, however, were Wood Storks documented to have nested there.

Wood Storks apparently moved to Cuthbert in the early 1930s. In 1932, 2000 birds were reported there without reference to actual nesting numbers. This colony was active in most years from 1932 to 1960 when a hurricane eliminated most of the island. Nesting Wood Storks returned there in 1963.

It was in this region (II) that a single report of a stork colony precipitated a vastly exaggerated view of historic population sizes. In the 1930s, known colony sites were being tended by wardens who, with few exceptions, were local backwoodsmen employed by the National Association of Audubon Societies (NAAS). This was a highly publicized effort, and most of the bird numbers reported to Association members in its journal originated with the wardens themselves or with NAAS officers on their annual inspections.

In 1933 an extraordinarily high number of birds was reported at a site we now call Old Lane River. This record originated with a report of NAAS Director of Sanctuaries Ernest G. Holt (1933a) on his annual inspection tour of 4–16 May 1933. He received the information in question from his wardens, who told him they had, just prior to his arrival, been guarding 50,000 Wood Storks in the Old Lane River Colony site. Holt (1933b) specifically published the following: "On Lane River, the wardens reported some 50,000 Wood Ibises, 40,000 Louisiana Herons, 40,000 Snowy Egrets, and 15,000 American Egrets breeding. The mortality here was excessively high, caused, by a terrible plague of mosquitoes." Holt himself did not see these large numbers of birds, but rather the wardens told him these numbers of birds had departed just days before his arrival. In an

unpublished report, Holt (1933a) did note carefully what he personally had observed. At Old Lane River he saw only several thousand Wood Stork fledglings and some birds of the other species. He estimated that Old Lane Colony covered 30 acres.

In evaluating this record we should consider several points. By his warden's estimates of 145,000 birds, only 0.8 $m^2$ of space per bird nest was available, and this necessarily included the water between the scattered islands. Such density of bird nests is not reasonable even in a multistoried colony site. The wardens with a couple of exceptions, such as E. J. Reimann, had little training or experience with quantified censusing. Few people did in the early 1900s. It should not be surprising that their reports of exceedingly large numbers were not confirmed by outside inspection (e.g., Holt 1933b). Reports from the wardens that they were guarding huge numbers of birds was eminently self-serving at a time of financial crisis in the NAAS. The previous year, all full-time wardens had been released except those in southern Florida, who that year had reported "staggering numbers" to New York (Holt 1932, Anon. 1933). By the next year funds had been found to fix their boats (Holt 1933b). Such factors cast substantial doubt on the wardens' reports of 1933, and it seems inappropriate to accept this record of 50,000 nesting Wood Storks or subsequent restatements and summaries using this record (e.g., Allen 1957, 1958, 1964; Sprunt and Kahl 1960; Robertson and Kushlan 1974).

After the 1930s, the numbers of birds nesting at Cuthbert Colony site decreased slowly. In 1950, the 3375 nests reported there were the highest for the southern colonies. This figure is derived from Cufaude and Brookfield's estimate that Cuthbert contained about 4500 nests, 75% of which were of Wood Storks (Brookfield 1950).

Nesting was first reported at East River, another site in Region II, in 1934, again in 1938, 1940 (Beard 1938, Vinten 1955, Storer 1957), and in nearly every year thereafter. The only numbers available for the 1940s were 300 nests in 1943 and 5500 birds in 1948. The latter estimate offered no information on how many storks were nesting. There are few records for the next decade, despite the creation of Everglades National Park. The East River Colony site was reported to contain 550 nests in 1959 and 650 in 1960. Nesting numbers increased in Region II through 1976 (Table 1).

Storks nested periodically at several sites along the southeastern coast in Region III beginning in 1948 at Joe Bay (Allen 1958). Little is known about these colony sites. In 1961 consistent nesting began at the Madeira Colony site, probably as a result of the hurricane adversely affecting the Cuthbert site island the previous year. A peak of 750 nests was reported at the Madeira site in 1966.

Wood Storks seldom have nested in large numbers in the inland south-

ern Everglades encompassed by Region IV. The earliest information of nesting was at Quok Creek (probably the Squawk Creek tributary to the Shark River) in 1930. Nesting was reported near here in 1933 and 1935 (Allen 1958). Wood Storks nested along the Rookery Branch tributary of Shark River intermittently in 8 of 50 years from 1933 onward. Although well known and visited in most years, this site was never a numerically important nesting site for Wood Storks.

We have no historic records of Wood Storks nesting in the more northern Everglades Region V. Nesting in the southern Big Cypress Swamp Region VI was sporadic.

Our consideration of the historic record of Wood Storks nesting at southern (Everglades-mangrove) sites (Regions I–VI) produced intriguingly few credible censuses, and overall low numbers relative to those commonly reported. Most reliable numerical estimates were in the hundreds with a few in the low thousands. The highest documentable number of *birds* observed near colony sites was in 1937 when 2500 birds were reported from Mud Lake site (Region I) and 1550 birds from the Cuthbert Site (Region II). This was the equivalent of 2025 pairs, but we found no documented evidence that all these birds nested. Ogden (1978b) stated that observers of Old Lane and East River colony sites "between 1934 and 1938 estimated a maximum of about 3000 stork nests," although giving no source for this figure. The highest historical nesting numbers were 3525 nests in 1950 (Table 1). In that each of these three totals is of similar magnitude, we conclude there is no evidence that the nesting population of Wood Storks in southern (Everglades-mangrove) colony sites exceeded about 3500 nests (7000 birds) historically. This is 30% fewer than the 10,000 estimated by Ogden and Patty (1981).

By far the longest run of quantitative information on nesting numbers is from the more northern Region VIII colonies in Corkscrew Swamp and the northern Big Cypress Swamp (Table 1). Nesting was documented as early as 1892 (Eliot 1892) and acceptable numbers are available for the Corkscrew site in the early 1900s. Baynard (1914) estimated 7000–8000 Wood Stork nests there in 1912; whereas, Phelps (1914) estimated "not less than 5000 pairs in 1913."

A larger estimate of 10,000 nests at a colony site in the Okaloacoochee Swamp by F. H. Kennard in 1926 (Bent 1926) is not credible. Kennard himself thought that it was "almost impossible to make any estimate of their numbers, even approximately without spending a couple of days counting their nests, but [that] there must have been several thousand flying about or perched." His accommodating guide, however, after climbing a convenient tree produced the estimate of 10,000 nests, a number that has been often repeated, usually as 20,000 adult storks.

Another repeated estimate of stork numbers in the Big Cypress is 30,000 Wood Storks reported from Corkscrew Swamp in the mid-1930s. We find no primary documentation for this claim. Thus, the largest documented estimate for Wood Storks nesting in the northern Big Cypress was the 8000 nests reported in 1912 by Baynard (1914), 20% less than that provided by Ogden and Patty (1981).

*Recent population estimates.*—The mid-1950s provide a convenient division between historic and recent records, because of the hiatus in numerical estimates available from this period, despite the establishment of Everglades National Park, which encompassed the southern colonies (Regions I–IV). Although data were lacking, it was the strong impression of conservationists that the Wood Stork population decreased drastically in this period because of drought (Buchheister 1960). This perceived decrease led to a heightened concern for the Wood Stork and inspired the initiation of surveys led by R. P. Allen, whose efforts provided fairly comprehensive information for 1959–1960. Aerial surveys and ground checks were initiated in 1958, a season described in detail by Allen (1958). The numbers were higher in 1959 and 1960 owing to his experience, better coverage, and better nesting conditions (Buchheister 1960), suggesting the latter years were more representative of the nesting population of Wood Storks at that time. Ogden and Nesbitt (1979) used these two years as their base of comparison to detect range-wide population decreases.

Allen found about 8500 Wood Stork nests in 1960 (Table 1). This is about the same as the highest population level we can document previously. Thus, it appears that the reported nesting failures of the 1950s did not adversely affect the Wood Stork population, and that conservationists' concerns for a decreasing population (e.g., Allen 1957) were illfounded.

The southern colonies (Regions I–IV) supported 1105 nests in 1959 and 1900 nests in 1960. These numbers are about half the values used by Ogden and Nesbitt (1979), perhaps because of a mix-up of nest numbers (i.e., pairs) and bird numbers. Thus, our maximum estimate for the southern colony sites for the late 1950s is 1900 nests.

There were gaps in census data from 1960 to the late 1960s, several years after substantial changes had occurred in water management in southern Florida. For 1967, we estimate 2100 pairs of Wood Storks in the southern colonies and 9400 pairs in southern Florida (Regions I–VII). This population estimate is higher than that documented in the two previous highest years, 1913 and 1960. Thus, we find no evidence to document a net decrease in the southern Florida Wood Stork population from 1913 through 1967.

In the following several years, the numbers of Wood Storks attempting

to nest in southern colonies (Regions I–IV) were low owing to a period of high water. Surveys during this time checked only major known colonies intermittently. In the early 1970s, monthly surveys were begun, and we undertook these comprehensively from 1975 through 1982. As a result, data from this period are relatively reliable, and comparable. Even with such comparable data it is difficult to trace trends, because in most years many birds apparently did not attempt to nest. As a result, we can evaluate population changes only by contrasting two years, such as 1967 to 1982, or by examining the trend for years of relatively high nesting effort, assuming that in such years most storks attempted to nest.

We can document that the number of Wood Storks attempting to nest decreased from 1967 to 1981–82, overall, and in most regions (Fig. 2). Four contrasts are of particular interest: (1) Corkscrew Swamp and northern Big Cypress (Region I), (2) the southern colonies in Everglades National Park (Regions I–IV), (3) the northern Everglades in the water reservoirs called conservation areas (Region V), and (4) southern Florida as a whole (Regions I–VII). From 1967 through 1981, Wood Storks nesting in the Corkscrew-northern Big Cypress region decreased by about 80%. From 1967 through 1982, the southern Everglades population (Regions I–IV) decreased by about 70%. Overall, then, the southern Florida population decreased by about 75% in 15 years from 1967 to 1981–82. More recently, the number of Wood Storks nesting in the northern Everglades increased from none to over 500, representing a shift of birds from the southern to northern Everglades. This shift increases the importance of maintaining the present, apparently appropriate, foraging and nesting conditions in the Everglades of Conservation Area 3A.

It is difficult to estimate the extant nesting population at the end of our study because nesting effort differed among regions in 1981 and 1982 (Table 1). In these two years Wood Stork nesting effort (nests) was: 1981—Lane River, 50; East River, 55; Cuthbert, 300; three colony sites in Conservation Area Three, 7, 2, 13; colony site in Conservation Area Two, 20, Two colony sites in Conservation Area One, 95, 160; Corkscrew, 1500. 1982—Lane River, 280; East River, 90; Cuthbert, 300; seven colony sites in Conservation Area Three, 75, 40, 380, 15, 9, 6, 24; Corkscrew, 18. Nesting effort was relatively high in the Corkscrew-northern Big Cypress Swamp (Region VII) in 1981 and in the southern and northern Everglades (Regions II and V) in 1982. To arrive at a total for southern Florida, we must assume no interchange between these areas, in order to permit addition of the regional totals for the separate years of high nesting effort. In this way we estimate the nesting Wood Stork population in southern Florida to be about 2700 pairs in 1981–82.

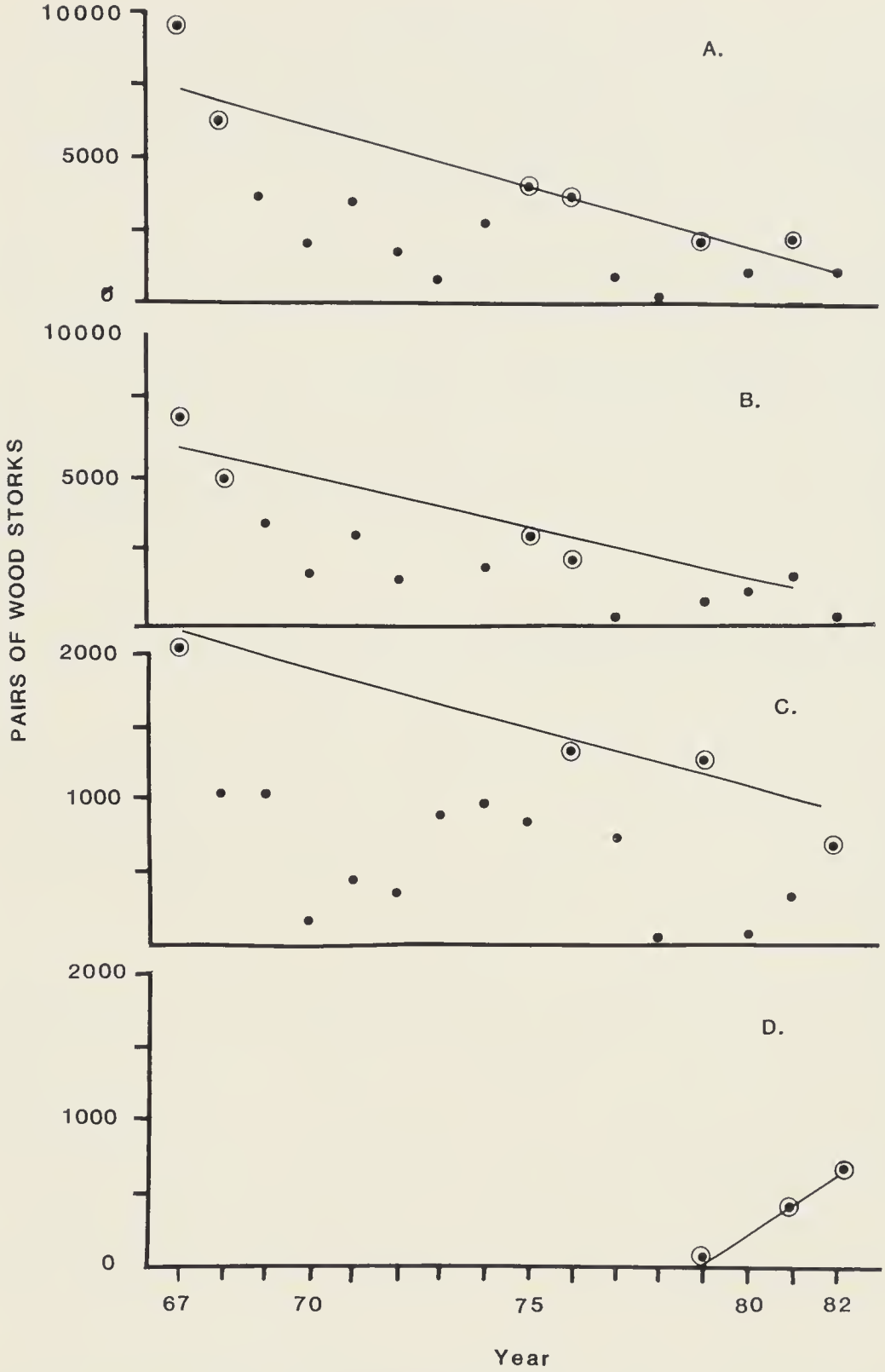


FIG. 2. Recent trends in the numbers of Wood Storks nesting in southern Florida: (A) Southern Florida, (B) Corkscrew-northern Big Cypress Swamp, (C) Southern Everglades, and (D) Northern Everglades. Double symbols indicate years of relatively high nesting effort. Trend lines follow the data for these high-effort years.

## DISCUSSION

*Colony sites.*—Wood Storks are well known for their colony-site tenacity, and indeed the Corkscrew site has been in use for over 70 years. Although storks tend to return to established sites year-after-year, site shifts do occur—usually over a period of several years. We have documented nesting at at least 51 sites in 102 years.

Some of these shifts have substantially redistributed the nesting population; notable is the abandonment of historic sites on Cape Sable (Region I). The principal reasons for the decrease in Wood Storks nesting on Cape Sable were the drainage canals, which were dug beginning in the 1920s (e.g., Holt 1929, Reimann 1940). The hurricane of 1936, the effects of which were exacerbated by the canals, caused massive vegetation changes, which affected several species. The Wood Stork decline was simultaneous with the well-known decrease of the Cape Sable Seaside Sparrow (*Ammodramus maritimus*) population (Kushlan and Bass 1983). Although the Alligator Lake colony site was altered, birds nested there and at other locations on the Cape afterward (Reimann 1940). Thus it was a change in foraging habitat rather than nest site unavailability that led to Wood Storks abandoning Cape Sable for nesting.

The long history and persistence of Wood Stork nesting on Cape Sable, covering 50 years, is notable. Over much of this period, Wood Stork colonies were not documented elsewhere in southern Florida outside the Big Cypress Swamp. This is not an oversight, in that wading bird colony sites elsewhere were well visited. It seems the Cape Sable cclony sites were the primary, if not only, Wood Stork nesting colonies near the southern Everglades before the 1930s.

Occupation of the famous sites at East River and Cuthbert, popularized by frequent visits of naturalists and ornithologists of the 1930s and 1940s, resulted from the movement of birds from Cape Sable to Hells Bay (Regions I to II) following the 1936 hurricane. A similar shift from Region II to III also was probably a result of this process, hurricanes in the early 1960s that followed construction of a canal in the 1950s by the National Park Service. Subsequent abandonment of Region III sites coincided with the loss of foraging habitat along the southeastern Florida coast. The most recent shift from southeastern coastal (Region II) to northern Everglades sites (Region V) clearly is in response to lowered food availability due to water management near southern colony sites (Kushlan et al. 1975).

Considering the many sites used for nesting in southern Florida ranging from coastal islands, clumps of mangrove trees, river-edge forest, Everglades tree islands, and cypress swamp; colony-site requirements of Wood Storks appear to be highly flexible. In fact, the number of suitable potential

colony sites in southern Florida seems nearly unlimited. All evidence suggests that patterns of food availability limit area use and colony-site tenacity (Kahl 1964, Kushlan et al. 1975, Ogden et al. 1976). Thus, conservation efforts aimed at protection, establishment, or re-establishment of specific nesting sites alone would be untenable in the long run. Suitable foraging sites rather than nesting sites seem to be the factor limiting the Wood Stork population.

*Nesting areas.*—Examining stork history on a regional basis provides insight into the relative importance of various areas in southern Florida. All evidence suggests that the Corkscrew-Big Cypress Area (Region VII) has always been far more important than the Everglades and coastal areas (Regions I–VI) in supporting the southern Florida population of nesting Wood Storks. Available censuses show more consistent yearly occupancy and higher nesting numbers in the Big Cypress Area than in the more southern colony sites.

Outside the Big Cypress Swamp, Wood Storks have seldom nested inland in large numbers in southern Florida. Similarly, storks have not nested along the west coast of Florida, although they feed there during most winters. Nesting in Florida Bay occurred only in 1949 and 1950 on Eagle Key. Nesting in southern regions for the most part has taken place along the edge of the southern Everglades drainage, on Cape Sable, and on the southeastern coast. The earliest nesting sites in this area were on Cape Sable, not in the Everglades marsh proper, although storks nesting there undoubtedly fed both in coastal mangrove swamps and the Everglades during drying conditions. The recent shift to northern Everglades colony sites is unprecedented, and therefore may well be a response to unnatural but relatively beneficial patterns of water level fluctuation in the northern marshes caused by current water management policy. Conservation of Everglades Wood Storks may require continuation of the unnatural enhancements of foraging conditions in the northern Everglades.

*The historic period.*—In evaluating the historic record we applied several criteria. The first two were objective, requiring a definite statement that nesting occurred and a definite statement of the number of birds, pairs, or nests involved. These do not seem unreasonably stringent to us, but even so their use eliminated some records of birds seen near a known or presumed colony site. We believe, however, that it is inappropriate to impose a second-hand interpretation of nesting on the actual information and to perpetuate such interpretations.

Many records appeared inconsistent or questionable in the light of other acceptable data. We found that most of these inconsistencies could be

resolved by evaluating the observer's credibility. For the most part, careful reading of accounts, usually more than one per record, provided sufficient information to evaluate statements. In nearly all cases of consequence, we found that these records were derived from the untrained and possibly self-serving statements of guides, wardens, and rangers. The primary, and historically tremendously important, responsibility of wardens was to provide the only protection available for these colony sites. Close readings of numerous warden reports convince us that, with very few exceptions (e.g., E. J. Reimann and C. Brookfield), quantification in these accounts is not reliable.

Other important sources of misinformation were the relatively recent censuses, mostly aerial surveys, which account for most modern records except for those from the Corkscrew site. Generally, such censuses were flown on a variable schedule. Most covered only known nesting sites and were done by persons of greatly different skill and experience. Only several recent years of consistent censuses of the southern colonies are available.

For these more recent data, derived from aerial censuses, the number of nests is inferred from the count of birds at the colony site or of birds standing in close proximity to each other and apparently paired. Important identification and counting errors were revealed in available data when we compared counts of different observers of the same colony or the same observer's counts on separate dates. Technique errors are substantial (Kushlan 1979), remain unquantified, and no error estimates have been derived. Such censuses are biased and at most represent the numbers of birds at the colony site at the time of census. Unfortunately, these censuses constitute the only historical data available in recent years and must be used to evaluate trends.

Year-to-year fluctuations of numbers of birds at colony sites suggest that not all birds nest each year and that they do not necessarily return to the same location in subsequent years. Thus, population trends can be evaluated only by comparing years of high colony occupancy over regions larger than a single colony site. The population being monitored, therefore, is the number of birds appearing at the colony site. It does not include the immature birds of several age classes, nor even adult birds that were not at the colony site during a census.

The potential errors involved with such aerial censuses should proscribe their continued use in monitoring Wood Storks. What is required for evaluating the population's status is not the number of birds showing up at a colony site but the per capita productivity of the breeding population, available only from detailed study on the ground.

*Population trends.*—Clearly the large numbers of storks reported from southern Florida as a whole have been based on a few unreliable records.

Allen (1958) used these in his historic population estimates, which were subsequently popularized by others. Sprunt and Kahl (1960), for example, reported that "in the mid-1930's there were lots of storks. According to Robert P. Allen, some 30,000 nested in the Corkscrew Swamp alone and another 50,000 at the heads of Shark and Lane rivers in what is now Everglades National Park. Other smaller colonies probably swelled the total to 100,000 or more birds." We have noted previously that the 50,000 estimate is untenable, and the 30,000 estimate is undocumented. The extra 20,000 was certainly a guess. Nonetheless, this 100,000 has often been taken to be the historic population size for south Florida (Allen 1958, Sprunt and Kahl 1960, Ogden and Nesbitt 1979), sometimes reduced to "over 75,000" (Robertson and Kushlan 1974), "75–100,000" (Parker 1985), or "75,000" (Ogden 1978a).

We have no credible evidence to suggest that the number of storks in southern Florida (Regions I–VII) exceeded the 8000 pairs reported in the northern Big Cypress Swamp and Corkscrew in 1912. The highest historic estimate available for southern colonies is 3500 pairs in 1950, which cannot be added to estimates at the Corkscrew site because of time gaps. In fact, we cannot verify an historic South Florida breeding population larger than that found as late as 1967. A larger population may have existed, without documentation, or it may have fluctuated more than can be verified. Considering the inherent error in the estimates, however, we are compelled to accept the fact that the maximum estimates for 1912, 1960, and 1967 are all about the same. We conclude that we have no historic evidence that southern Florida supported a Wood Stork nesting population larger than that of 1967, when we have documentation of 9400 pairs.

The southern Florida Wood Stork population has been reported to be decreasing for the past 30 years (e.g., Allen 1958). In nearly all cases the decrease is documented through comparison of presumed populations in the 1930s. Ogden and Patty's (1981) evaluation, used by the U.S. Fish and Wildlife Service (1984), concluded that the U.S. population decreased from 20,000 breeding pairs during the 1930s to approximately 4800 in 1980. Their historic number included 5000 pairs in Everglades colonies (our Regions I–IV) and 10,000 in Big Cypress Swamp (Our Region VII). Our highest credible estimate for southern Florida (Regions I–VII) is two-thirds of that estimate.

Ogden and Nesbitt (1979) considered the surveys by Allen in the late 1950s to be a suitable historic baseline. Our review however, indicates that maximum documentable population size was in 1967, rather than in 1959–60. It is during the past 15 years, rather than 22 years, that we can see a clear change in Wood Stork numbers in southern Florida. Over-

all, by 1981–82 the southern Florida population (Regions I–VII) had decreased to about 25% of its level approximately 15 years previously, to a recent nesting population of about 2700 pairs.

The lack of documentably high historic numbers actually should be of little consequence to current Wood Stork conservation, which scarcely needs to appeal to the historic (or really "prehistoric") occurrence of 100,000, 75,000, or even 30,000 storks. So many changes have occurred in southern Florida since the 1930s that any numbers from that era could have no applicability to current conservation efforts.

Unlike the previously presumed decreases since the 1930s, decreases over the past decade and a half can be linked to potentially reversible management practices, specifically water management in Everglades National Park and drainage in the Big Cypress Swamp (Kushlan et al. 1975, Browder 1976). Birds nesting in the Big Cypress Swamp appear to be suffering from loss of suitable foraging habitat. In recent years southern Everglades Wood Storks have nested successfully only in the few years when the water levels fell substantially during the dry season, (i.e., 1967, 1974, and 1975). In fact, nesting failure in southern Everglades colonies can be attributed directly to maintenance water levels that were too high in spring and to decreased rates of drying in the southern Everglades (Kushlan et al. 1975). To protect the Wood Stork in southern Florida, the southern Everglades must be permitted to dry seasonally, and overdrainage of the Big Cypress Swamp must be abated.

It should be of considerable value to Wood Stork conservation to realize that population decreases in this species in southern Florida are of recent occurrence, on the order of 75% rather than 95%, and have been caused by understandable alteration in feeding habitat. In the Everglades, and to some extent in the Big Cypress Swamp, management to enhance Wood Stork habitat is possible. Meanwhile, southern Everglades storks are responding to environmental changes by shifting colony sites to the northern Everglades where water management actions have apparently provided more suitable foraging habitat than further south.

Allen et al. (1958), after describing the earlier nesting 25 years before of up to 65,000 Wood Storks in southern Florida, stated that ". . . the fact that they once existed—such a relatively short time ago—should not be thrust aside or forgotten. If we are to find a way to insure the permanent survival of the Wood Storks that remain, we must know what destroyed these immense congregations of the recent past." We suggest that, rather than concentrating on questionable data from the past, attention should be paid to managing present stork foraging habitat in the southern Florida wetlands.

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# THE EVOLUTION OF REVERSED SEXUAL DIMORPHISM IN OWLS: AN EMPIRICAL ANALYSIS OF POSSIBLE SELECTIVE FACTORS

HELMUT C. MUELLER[1]

ABSTRACT.—No less than 20 hypotheses have been proposed to explain reversed sexual dimorphism (RSD) in raptorial birds. I have generated a prediction from each of these hypotheses and tested the prediction using the available information and nonparametric statistics. RSD correlates significantly only with female dominance in intraspecies interactions and with prey type. Unfortunately, the data on dominance interactions are limited, but the best working hypothesis appears to be that RSD has evolved primarily as a result of epigamic selection, with female dominance facilitating pair formation and maintenance. Prey specialization appears merely to influence the degree of, and does not cause, RSD. Most species of owls are specialists on either invertebrates or small mammals. Specialists on invertebrates show little RSD and specialists on small mammals show moderate to high RSD. *Received 22 Feb. 1985, accepted 31 Jan. 1986.*

Much has been published on reversed sexual dimorphism (RSD) in Falconiformes in the past two decades (e.g., Newton 1979, Andersson and Norberg 1981, Cade 1982, Mueller and Meyer 1985). In contrast, only two major works have dealt with RSD in Strigiformes: the pioneering work of Earhart and Johnson (1970) and the monograph of Snyder and Wiley (1976), which concentrated on Falconiformes and gave owls only perfunctory treatment. Both of these studies deal mainly with the correlation between RSD and prey type. It appears timely to reexamine the possible adaptive functions of RSD in owls with new data and in the light of recent analyses of Falconiformes. The primary premise in my analysis is that if a given trait was important in the evolution of RSD it should be exhibited to a greater degree in highly dimorphic species than in less dimorphic ones. My approach is empirical, using the most rigorous statistical test permitted by the data available.

No fewer than 20 hypotheses have been proposed to explain RSD in raptorial birds. Most of the recent attempts to explain RSD in raptors have involved combining several of the many hypotheses. Each hypothesis, however, must be tested separately and I thus provide a list, along with predictions formulated from each hypothesis. All but one of these hypotheses can be grouped into three categories: (1) ecological hypotheses, (2) sex-role differentiation hypotheses, and (3) behavioral hypotheses.

[1] Dept. Biology, Univ. North Carolina, Chapel Hill, North Carolina 27514.

### ECOLOGICAL HYPOTHESES

There are several of these, but all share the premise that RSD has evolved to permit the sexes to capture different sizes of prey, thus reducing competition between the sexes and allowing a pair to exploit a wider range of sizes of prey (Brüll 1937, Hagen 1942, Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Newton 1979, Andersson and Norberg 1981). A prerequisite (but not proof) for these hypotheses is that the sexes take different sizes of prey. Selander (1972) has stated: "Only when trophic structures alone are modified can we conclude that the dimorphism results primarily or wholly from selection for differential niche utilization." This can be tested by comparing RSD in trophic structures with RSD in body size and nontrophic structures.

### SEX-ROLE DIFFERENTIATION HYPOTHESES

The difference in size permits the sexes to perform better various activities associated with reproduction than if the sexes were monomorphic and shared breeding duties equally.

*Egg size.*—Large females can lay larger eggs than smaller individuals (Reynolds 1972, Selander 1972, Schantz and Nilsson 1981, Cade 1982). This leads to the prediction that species with high RSD should lay relatively large eggs.

*Follicle protection.*—Large females provide a better cushion for developing eggs than smaller ones (Walter 1979). A relationship between RSD and egg size or clutch size might be considered as evidence for this hypothesis.

*Breeding increment in weight.*—Females of many species increase in weight prior to egg laying. Wheeler and Greenwood (1983) have suggested that large females are better able to carry this increment and continue to hunt elusive prey. I will test this hypothesis using their method: a linear regression of female weight plus egg weight on dimorphism in wing length in those species with similar predatory habits.

*Incubation.*—Large females incubate more efficiently than smaller individuals (Snyder and Wiley 1976, Cade 1982). Females should perform a greater share of incubation in species showing high RSD than in those that are less dimorphic.

*Nest protection.*—Large females are more effective in deterring predators than smaller individuals (Storer 1966, Reynolds 1972, Snyder and Wiley 1976, Andersson and Norberg 1981, Cade 1982). Females of highly dimorphic species should perform a greater proportion of nest defense than those of less dimorphic species.

*Territorial defense.*—Small, agile males are better in the aerial defense of territory against conspecifics than larger, less agile individuals (Schmidt-

Bey 1913, Nelson 1977, Widen 1984). As it is unlikely that more than a few species of owls engage in aerial defense of territory (Amadon 1959), this hypothesis appears to be invalid for owls (Widen 1984).

*Feeding efficiency.*—Large females are more efficient at dismembering prey and feeding bits to small young (Andersson and Norberg 1981). Females in species with high RSD should perform a higher proportion of direct feeding of young than those in species with low RSD.

*Foraging interference.*—It is more efficient for only one member of the pair to hunt alert and agile prey than to have two birds moving about alerting prey and thus interfering with each other (Andersson and Norberg 1981). This hypothesis leads to the prediction that the male, who is the primary provisioner, should do proportionally more of the hunting in highly dimorphic than in less dimorphic species.

*Energy conservation.*—Energy consumption is a function of body size and small males thus might forage, and provide food for the young, more efficiently than large females (Reynolds 1972, Mosher and Matray 1974, Balgooyen 1976). However, in-flight metabolism of Common House-Martins (*Delichon urbica*) does not vary with body size (Bryant and Westerterp 1982), and the use of differences in resting metabolism (Mosher and Matray 1974) as a basis for this hypothesis is questionable. However, if smaller individuals require less energy in flight than larger ones, then males should forage more in highly dimorphic species than in less dimorphic ones.

*Pyramid of numbers of prey sizes.*—Small prey are more abundant than large prey, and small males should do most of the hunting until the food demands of the young become sufficiently great, and the supply of small prey sufficiently depleted, at which time the female must join in hunting, capturing, and delivering larger prey (Storer 1966, Reynolds 1972, Schantz and Nilsson 1981). Thus, provisioning by males should be greater in species with high RSD than in those with low RSD.

## BEHAVIORAL HYPOTHESES

*Sociability.*—Coloniality may inhibit the evolution of RSD (Walter 1979). Another possibility is that colonial species may be less dimorphic than noncolonial species because communal defense against predators reduces the need for larger females (Snyder and Wiley 1976). Either hypothesis predicts lower RSD in colonial species than in noncolonial ones.

The remaining behavioral hypotheses hold that RSD has evolved to facilitate female dominance of the male.

*Anticannibalism.*—Large females prevent small males, who are presumed to have less of a "parental instinct," from eating their young (Hagen 1942, Amadon 1959). This leads to the prediction that males should

perform less brooding of young in highly dimorphic than in less dimorphic species.

*Pair-bonding.*—Formation and maintenance of pairbonds is facilitated by female dominance and large size facilitates dominance (Perdeck 1960, Amadon 1975, Ratcliffe 1980, Cade 1982, Smith 1982, Mueller and Meyer 1985). This hypothesis predicts that females should be more dominant in species with high RSD than in those with low RSD.

*Role-partitioning.*—Female dominance excludes the male from incubation, brooding, etc. and forces him into the role of provider of food (Cade 1960, 1982; Monneret 1974).

*Female selection of males who are good provisioners.*—Male raptors begin to provision females well in advance of egg laying (Safina 1984). This could allow the female to assess the male's quality as a provider. Safina proposes that females select males that are frequent providers. He argues that small males can provide food to females more frequently than large males because (1) size of prey is correlated with size of raptor, particularly in species that pursue agile prey, and (2) small prey is more abundant and thus captured more frequently. This hypothesis predicts that smaller owls should take smaller prey than large owls.

There is one remaining hypothesis that does not fit into the above categories. It is also unique in that it limits, rather than promotes, RSD. Nesting in cavities inhibits the development of RSD (Walter 1979). Cavities, particularly those produced by woodpeckers, are available only in a limited variety of sizes. Cavities in general are scarce in comparison to other nest sites. This scarcity of sizes of cavities might inhibit evolution of large females.

## MATERIALS AND METHODS

Wing measurements (chord) of North American owls are taken from Earhart and Johnson (1970) and weights are from Dunning (1984), except for the Boreal Owl, where I have chosen to use the rather small sample of North American weights given in Earhart and Johnson rather than the European weights given by Dunning. Data on food habits of North American owls were taken from Snyder and Wiley (1976). Information on clutch size, behavior, and other aspects of the life histories of North American owls were taken from Bent (1938). Weights, wing measurements, and data on food habits of European owls were taken from Mikkola (1983). Other information on European owls was obtained from Glutz and Bauer (1980). Egg weights were taken from Schönwetter (1967). I have chosen the best available secondary sources of data in a deliberate effort to avoid biases that might result from my own summarization of primary sources. The data are presented in Tables 1 and 2.

This paper attempts to test as many hypotheses on RSD as possible, using, primarily, nonparametric statistics (Siegel 1956). Unless otherwise indicated, probability values given are one-tailed. I have chosen to treat the North American and European owls separately in part because the quality of the data available is quite different for the two continents, and

also because there are considerable regional variations in the biology of at least several species of owls.

In Tables 1 and 2, RSD is expressed simply as the mean for males divided by the mean for females. For weights, I have used the cube root in calculating the dimorphism ratio, following time-honored convention and thus permitting some comparison with the ratio derived from wing chord.

## RESULTS

### Ecological Hypotheses

Data permitting a comparison of the sizes of prey taken by the sexes in owls are available for only 3 species (Mikkola 1983: table 55). Mikkola's data are from Finland, where all three species show great overlap in geographic range, habitat preference, and are known to breed in the vicinity of each other. Mikkola's prey sizes are estimates based on the average weights of the prey species and the most appropriate way to deal with such estimates is to place them in size classes (Storer 1966). The female Boreal Owl takes significantly larger prey than the male, ($\chi^2 = 4.09$, $P < 0.05$), but there are no significant differences between the sexes in size of prey in the Great Gray ($\chi^2 = 3.84$, $P > 0.05$) or Ural Owls ($\chi^2 = 3.42$, $P > 0.06$). The differences in the last two species are close to significance, but in the Ural Owl it is the male that takes larger prey than the female. The Boreal Owl exhibits high RSD, particularly in weight, but less so than the Great Gray Owl (Table 2). Both sexes of both species of *Strix* are considerably larger than female Boreal Owls, with average weights ranging from 4.3× greater for male Ural owls to 7.4× for female Great Gray Owls. A comparison of the size of prey taken by the female Boreal Owl with both sexes of the other two species shows that only the male Ural Owl captures significantly larger prey ($\chi^2 = 7.27$, $P < 0.01$). A similar comparison for the male Boreal Owl shows that only the female Great Gray Owl captures significantly larger prey ($\chi^2 = 4.08$, $P < 0.05$). The apparent inconsistencies in the above are largely the result of small sample sizes for the Boreal Owl and the way cells must be combined to yield a minimum expected value of 5 for a chi-square test. Overall, the evidence strongly suggests that there are no real differences in the size of prey taken within or between these three species of owls. It is remarkable that the very large female Great Gray Owl not only captures prey of the same size as the small female Boreal Owl, but there also is no difference in the composition of the species taken (Spearman rank correlation coefficient, $r_s = 0.6192$, $P < 0.04$).

Earhart and Johnson (1970) report a significant difference in the proportions of mammals and birds taken by male and female Northern

TABLE 1

SEXUAL DIMORPHISM IN SIZE AND ASPECTS OF THE BIOLOGY OF NORTH AMERICAN OWLS

| | Dimorphism[a] | | | | Food[d] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\sqrt[3]{\text{Weight}}$ | Wing | Wing loading[b] | Mean species weight[c] | % Mammals | % Birds | % Invert. | Clutch size | Egg weight |
| Common Barn-Owl (*Tyto alba*) | 0.966 | 0.986 | 0.928 | 466.1 | 91.4 | 6.9 | 1.6 | 6 | 25.5 |
| Flammulated Owl (*Otus flammeolus*) | 0.980 | 1.012 | 0.920 | 55.6 | 0 | 0 | 100 | 3.5 | 10.3 |
| Eastern Screech-Owl (*O. asio*) | 0.951 | 0.975 | 0.906 | 180.5 | 65.5 | 3.3 | 30.7 | 3.6 | 17.4 |
| Western Screech-Owl (*O. kennicotti*) | 0.951 | 0.967 | 0.921 | 143.0 | 65.5 | 3.3 | 30.7 | 3.7 | 18.0 |
| Whiskered Screech-Owl (*O. trichopis*) | 0.971 | 0.995 | 0.925 | 88.4 | 1.8 | 0.4 | 97.4 | 3.2 | 14.1 |
| Great Horned Owl[e] (*Bubo virginianus*) | 0.912 | 0.952 | 0.845 | 1308.7 | 77.6 | 6.1 | 14.7 | 2.7 | 66.5 |
| Snowy Owl[e] (*Nyctea scandiaca*) | 0.942 | 0.937 | 0.953 | 1802.7 | 78.0 | 21.3 | 0.1 | 6 | 63.5 |
| Northern Hawk-Owl (*Surnia ulula*) | 0.954 | 0.977 | 0.909 | 322.2 | 93.7 | 3.8 | 0 | 5 | 21.6 |
| Northern Pygmy-Owl (*Glaucidium gnoma*) | 0.947 | 0.958 | 0.924 | 67.5 | 23.3 | 12.8 | 61.4 | 3.5 | 9.5 |
| Ferruginous Pygmy-Owl (*G. brasilianum*) | 0.935 | 0.983 | 0.847 | 68.3 | — | — | — | 3.5 | 8.3 |
| Elf Owl (*Micrathene whitneyi*) | — | 0.985 | — | 41.0 | 1.9 | 0 | 98.1 | 3.2 | 7.3 |
| Burrowing Owl (*Athene cunicularia*) | 1.017 | 1.017 | 1.018 | 154.6 | 6.9 | 0.3 | 90.9 | 6.8 | 11.1 |
| Spotted Owl (*Strix occidentalis*) | 0.970 | 0.978 | 0.956 | 609.7 | 37.5 | 4.5 | 57.4 | 2.3 | 47.0 |
| Barred Owl (*S. varia*) | 0.924 | 0.973 | 0.833 | 716.4 | 76.0 | 5.8 | 15.8 | 2.3 | 47.2 |
| Great Gray Owl[e] (*S. nebulosa*) | 0.897 | 0.956 | 0.789 | 1116.4 | 93.3 | 6.7 | 0 | 2.6 | 52.0 |
| Long-eared Owl[e] (*Asio otus*) | 0.958 | 0.991 | 0.894 | 262.4 | 97.1 | 2.3 | 0.6 | 4.5 | 23.3 |
| Short-eared Owl[e] (*A. flammeus*) | 0.941 | 0.995 | 0.841 | 346.4 | 94.5 | 4.0 | 1.5 | 6 | 21.3 |
| Boreal Owl (*Aegolius funereus*) | 0.900 | 0.926 | 0.849 | 120.6 | 93.6 | 6.4 | 0 | 5 | 12.7 |
| Northern Saw-Whet Owl (*A. acadicus*) | 0.938 | 0.951 | 0.912 | 82.9 | 96.8 | 1.6 | 1.4 | 5.5 | 10.2 |

[a] Dimorphism = ♂♂/♀♀.
[b] Wing loading. An index of (♂♂ weight/♂♂ wing$^2$)/(♀♀ weight/♀♀ wing$^2$).
[c] Mean species weight (g) = $\bar{x}$ ♂♂ weight + $\bar{x}$ ♀♀ weight/2.
[d] Food. Percent of total food items. The percent of lower vertebrates is not presented. It can be obtained by adding the percentages given and subtracting from 100.
[e] Breeds in open nests.

TABLE 2

SEXUAL DIMORPHISM IN SIZE AND ASPECTS OF THE BIOLOGY OF EUROPEAN OWLS[a]

| | Dimorphism | | | | Food | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\sqrt[3]{\text{Weight}}$ | Wing | Wing loading | Mean species weight | % Mammals | % Birds | % Invert. | Clutch size | Egg weight |
| Common Barn-Owl | 0.952 | 0.997 | 0.868 | 337.0 | 95.0 | 2.7 | 0.8 | 4.6 | 21.0 |
| European Scops-Owl (*Otus scops*) | 0.950 | 0.977 | 0.898 | 104 | — | — | — | 3.5 | 12.4 |
| European Eagle-Owl[b] (*Bubo bubo*) | 0.960 | 0.932 | 0.856 | 2665.5 | 59.7 | 35.8 | 0.4 | 2.7 | 77.5 |
| Snowy Owl[b] | 0.917 | 0.926 | 0.899 | 1982.5 | 97.8 | 1.6 | 0.1 | 8 | 63.5 |
| Northern Hawk-Owl | 0.955 | 0.992 | 0.885 | 303.0 | 96.2 | 2.7 | <1.1 | 7 | 21.8 |
| European Pygmy-Owl (*Glaucidium passerinum*) | 0.948 | 0.942 | 0.960 | 62.0 | 62.3 | 36.8 | <0.9 | 5 | 9.0 |
| Little Owl (*Athene noctua*) | 0.994 | 0.988 | 1.006 | 173.5 | 14.9 | 0.7 | 83.7 | 4.1 | 15.8 |
| Tawny Owl (*Strix aluco*) | 0.933 | 0.956 | 0.888 | 528.5 | 80.3 | 9.2 | 6.0 | 3.24 | 39.5 |
| Ural Owl (*S. uralensis*) | 0.939 | 0.966 | 0.887 | 795.5 | 78.6 | 14.2 | 2.2 | 3.65 | 50.0 |
| Great Gray Owl[b] | 0.888 | 0.931 | 0.888 | 1056.5 | 98.5 | 1.0 | 0.1 | 4.05 | 53.0 |
| Long-eared Owl[b] | 0.959 | 0.987 | 0.882 | 307.5 | 92.0 | 7.7 | 0.2 | 4.5 | 23.0 |
| Short-eared Owl | 0.948 | 0.992 | 0.866 | 380.5 | 97.6 | 1.1 | 1.1 | 6.85 | 21.3 |
| Boreal Owl | 0.901 | 0.933 | 0.840 | 145.5 | 94.5 | 5.4 | 0.1 | 5.0 | 12.5 |

[a] Conventions as in Table 1.
[b] Breeds in open nests.

Pygmy-Owls; however, all of my attempts to replicate their calculations show no significant difference.

Although too few data are available for a conclusive answer to the question as to whether trophic appendages are more dimorphic than body size or nontrophic appendages in owls, a preliminary analysis is possible, Mlikovsky and Piechocki (1983) present 7 measurements for 6 species of European owls: (1) body weight, which I express as the cube root to permit comparison with linear measurements; (2) wing arc (flattened wing); (3) tail length; (4) tarsus length; (5) foot size, the distance between the tips of the claws of the middle and hind toe, with the foot outstretched; (6) beak length, including cere; (7) beak depth, the vertical thickness of the beak measured in a straight line at the edge of the feathers. RSD values for these seven measurements are presented in Table 3.

To compare the relative dimorphism of the various structures and of body size, I looked at the number of species in which RSD in one structure exceeds RSD in another structure (Table 4). No clear picture emerges; only one structure appears to be more dimorphic than any other; beak depth is significantly more dimorphic than tail length in all six species (sign test, $P = 0.016$). Foot size, the measure of the most probable trophic appendage (Mueller and Meyer 1985) exhibits greater dimorphism in only half of the comparisons with other measurements.

A starting point for most ecological hypotheses is to show that RSD is correlated with the type of prey taken, and such evidence does exist for owls (Tables 1 and 2). RSD is correlated with the proportion of vertebrates in the diet: weight, North America, $r_s = 0.6519$, N = 16, $P < 0.004$; Europe, $r_s = 0.5785$, N = 12, $P < 0.03$; wing, North America, $r_s = 0.5785$, N = 17, $P < 0.02$; Europe, $r_s = 0.5901$, N = 12, $P < 0.03$. There is no consistent correlation between RSD and birds or mammals in the diet. RSD is correlated with percent birds in the diet for North American owls: weight, $r_s = 0.5676$, $P < 0.02$; wing, $r_s = 0.6233$, $P < 0.005$; but there is no correlation between birds consumed and RSD in European owls: weight, $r_s = 0.1926$, $P > 0.26$; wing, $r_s = 0.1807$, $P > 0.24$. RSD is correlated with mammals taken only with weight for North American owls, $r_s = 0.5676$, $P < 0.02$, and not with wing, $r_s = 0.3789$, $P > 0.06$; and neither with weight, $r_s = 0.2867$, $P > 0.16$, nor wing, $r_s = 0.0385$, $P > 0.45$, for European owls. The correlation between birds in the diet and RSD in North American owls is of dubious importance. Half of the species consume less than 4% birds and only 11.8% take more than 10% birds (Table 1). In contrast half the species consume more than 77% mammals and 41.2% take more than 90% mammals. The situation is similar with European owls, where half the species consume less than 3% birds and only 25% take more than 10% birds (Table 2). Mammals constitute more than

TABLE 3

REVERSED SEXUAL DIMORPHISM OF BODY SIZE AND VARIOUS STRUCTURES IN SOME EUROPEAN OWLS[a]

| Species | $\sqrt[3]{\text{weight}}$ | Wing | Tail | Tarsus | Foot | Beak | |
|---|---|---|---|---|---|---|---|
| | | | | | | Length | Depth |
| Common Barn-Owl | 0.982 | 0.999 | 0.992 | 1.009 | 0.996 | 0.975 | 0.973 |
| European Eagle-Owl | 0.893 | 0.946 | 0.938 | 0.987 | 0.909 | 0.861 | 0.932 |
| Little Owl | 1.015 | 0.978 | 0.985 | 0.927 | 1.027 | 1.012 | 0.984 |
| Tawny Owl | 0.916 | 0.957 | 0.969 | 0.981 | 0.942 | 0.924 | 0.939 |
| Long-eared Owl | 0.946 | 0.984 | 0.984 | 0.946 | 0.934 | 0.995 | 0.965 |
| Short-eared Owl | 0.990 | 1.030 | 1.007 | 0.986 | 0.890 | 0.892 | 0.938 |

[a] Data from Mlikovsky and Piechocki (1983). Measurements of the structures are described in the text.

90% of the diet of 58.3% of the European species of owls. It is enigmatic that European owls consume significantly more birds than North American owls (Mann-Whitney *U*-test, $P < 0.05$) but show no correlation between RSD and birds in the diet.

Snyder and Wiley (1976) found that birds yielded the highest correlation between diet and a composite index of RSD for a combined sample of North American Falconiformes and owls. Johnson (1978), in a review of Snyder and Wiley's monograph, notes that if Falconiformes are divided into two approximately equal subsamples, one containing species with low RSD and the other those with high RSD, then there is a correlation between birds consumed and RSD only in the subsample with high RSD. As Johnson notes, there appears to be an abrupt threshold below which birds in the diet have no influence on RSD. Johnson's method is even more revealing for owls.

Only 4 species of North American owls consume more than 90% invertebrates: the Flammulated, Whiskered Screech-, Elf, and Burrowing Owls. There is no correlation between RSD in wing and diet in these 4 species: vertebrates, $r_s = -0.4000$; birds, $r_s = -0.2108$; mammals, $r_s = -0.2000$ (with N = 4, $r_s$ must be 1.0 for $P = 0.05$). No weights are available to calculate RSD for the Elf Owl, and a sample size of 3 is inadequate to calculate $r_s$. However, there would be no correlation between RSD and weight for these 4 species, regardless of what might be the RSD for the Elf Owl, because the Burrowing Owl has the lowest rank for RSD and the highest rank for vertebrates, birds, and mammals in the diet. There is also no correlation between RSD and diet in the remaining 13 species: vertebrates, weight, $r_s = 0.3646$, $P > 0.10$; wing, $r_s = 0.2707$, $P > 0.18$; birds, weight, $r_s = 0.1978$, $P > 0.25$; wing, $r_s = 0.3407$, $P > 0.13$; mammals, weight, $r_s = 0.1813$, $P > 0.27$; wing, $r_s = -0.1374$, $P > 0.35$.

TABLE 4

COMPARISONS OF REVERSED SEXUAL DIMORPHISM OF TROPHIC AND OTHER STRUCTURES IN 6 SPECIES OF EUROPEAN OWLS

| | Beak length | Foot | $\sqrt[3]{\text{Weight}}$ | Tarsus | Tail | Wing |
|---|---|---|---|---|---|---|
| Beak depth | 3[a] | 3 | 3 | 4 | 6 | 5 |
| Beak length | | 4 | 4 | 4 | 4 | 4 |
| Foot | | | 2 | 5 | 4 | 5 |
| Weight | | | | 3[b] | 5 | 5 |
| Tarsus | | | | | 3 | 3 |
| Tail | | | | | | 4[b] |

[a] The number of species showing greater dimorphism in the measurement listed on the left than in the measurement listed above.
[b] One tie, reducing maximum possible N = 5.

The species of North American owls that consume more than 90% invertebrates show low RSD in both wing and weight. The remaining species, which consume a mean of 85.8% vertebrates (range = 38.1–100%), 6.6% birds (range = 1.6–21.3%), and 78.3% mammals (range = 23.3–97.1%), are at least moderately dimorphic.

A similar analysis of European owls produces basically similar, but slightly less distinct results. The Little Owl is the only European Owl with a large proportion of invertebrates in its diet (83.7%). It is also the least dimorphic in weight, and its removal from the sample leaves no significant correlation between vertebrates consumed and RSD in weight in the remaining 11 species ($r_s = 0.4506$, $P > 0.06$). These 11 species consume a mean of 86.6% (range = 59.7–98.5) mammals, 10.7% (range = 1.0–36.8) birds, and 1.3% (range = 0.1–6.0) invertebrates.

The correlation between RSD in wing and vertebrates in the diet persists in this sample of 11 species ($r_s = 0.5853$, $P < 0.03$). Indeed, it is necessary to divide the sample into the 5 species ranked lowest and the 7 ranked highest in consumption of vertebrates to eliminate correlations with RSD in wing in both subsamples ($r_s = -0.6842$, $P > 0.05$; $r_s = 0.4818$, $P > 0.05$; respectively). The 7 species in the subsample with a high consumption of vertebrates are not significantly more dimorphic in RSD in wing than the 5 species in the low subsample (Mann-Whitney $U = 7$, $P > 0.10$, two-tailed). The correlation between RSD in wing and vertebrates consumed thus appears to be the result of combining a tendency to a negative correlation in the low subsample with a tendency to a positive correlation in the high subsample. The division into subsamples leaves us with no consistent difference in the type of prey taken: invertebrates, low sample mean 18.8% (range = 1.1–83.7), high sample mean 0.4% (range = 0.1–

<0.9); mammals, low sample mean 73.5% (range = 14.9–97.6), high sample mean 73.0% (range = 59.7–98.5); birds, low sample mean 5.6% (range = 0.7–14.2), high sample mean 13.0% (range = 1.0–36.8).

Andersson and Norberg (1981) have noted that size affects flight performance of birds, particularly in such aspects as pursuit of prey, and have suggested that this might be an important factor in the evolution of RSD. Schantz and Nilsson (1981) believe that an important factor in the evolution of RSD is the relative ability to transport large prey. These aspects of flight performance are greatly influenced by wing loading. There is virtually no information available on sex differences in wing loading in owls. A crude index of wing loading can be obtained by dividing weight by the square of wing length, and this index is probably adequate for ranking species in respect to RSD in wing loading (Tables 1 and 2). This index of RSD in wing loading is correlated with vertebrates in the diet of both European and North American owls ($r_s = 0.5750$, $P < 0.03$; $r_s = 0.4897$, $P < 0.03$; respectively). The index is also correlated with mammals consumed for North American owls ($r_s = 0.5118$, $P < 0.02$), but not for European owls ($r_s = 0.4196$, $P > 0.08$). There is no correlation with birds in the diet (Europe, $r_s = -0.0911$, $P > 0.40$; North America, $r_s = 0.1132$, $P > 0.32$). Deletion of the Little Owl, the only specialist on invertebrates in the European owls, results in no significant correlation between vertebrates in the diet and RSD in the wing-loading index in the remaining sample ($r_s = 0.4510$, $P > 0.08$). Removal of the 3 species of specialists on invetebrates from the North American sample results in no correlation between RSD in wing-loading index and vertebrates ($r_s = 0.3591$, $P > 0.10$) or mammals ($r_s = 0.3681$, $P < 0.10$) in the diet of the remaining 13 species.

## Sex-role Differentiation Hypotheses

*Egg size.*—Although it is true that larger owls lay larger eggs than smaller owls, it is also true that the eggs of large owls are smaller, relative to body weight, than the eggs of smaller owls (Tables 1 and 2). This makes it extremely difficult to test the hypothesis that RSD has evolved to permit females to lay larger eggs. I propose the following solution to the problem. A regression of egg weight (y) on mean body weight (x) of females yields a "predicted" egg weight for each species. These regressions are excellent fits to the data: North American owls, $y = 0.033x + 10.67$, $r = 0.9479$, $P < 0.0001$; European owls, $y = 0.023x + 14.87$, $r = 0.9426$, $P < 0.0001$. The observed values for egg weight can be greater or less than the weight "predicted" by the regression line. The difference between observed and expected values, expressed as a percentage of mean body weight for the species, should be correlated with RSD if highly dimorphic species lay

relatively larger eggs than less dimorphic species. There is no such correlation (North American owls, weight, $r_s = -0.0176$, $P > 0.45$; wing, $r_s = 0.0062$, $P > 0.45$; European owls, weight, $r_s = 0.3242$, $P > 0.10$; wing, $r_s = 0.1871$, $P > 0.25$).

*Clutch size.*—There is no correlation between RSD and clutch size in owls. In the North American species: $r_s = 0.2729$ for weight, $P > 0.12$; $r_s = -0.0960$ for wing, $P > 0.35$. In the European owls: $r_s = 0.1678$ for weight, $P > 0.28$; $r_s = -0.0165$ for wing, $P > 0.47$.

*Breeding increment in weight.*—Wheeler and Greenwood (1983) divide the Falconiformes into four categories of flight performance in pursuit of prey. All of the North American owls except the Flammulated, Whiskered Screech-, Elf, and Burrowing owls fit into their "high" category: "aerial hunters of fast moving prey on the ground (mainly birds and mammals) which is usually taken on the ground or in the early stages of flight." A linear regression of the inverse of RSD of wing (y) on female weight plus egg weight divided by female weight (x) yields: $y = -0.060x + 1.10$, $r_s = -0.0834$, $P > 0.60$; two-tailed. All of the European owls except the Little Owl fit into the "high" category of Wheeler and Greenwood. A linear regression of the inverse of RSD on breeding increment on these 11 species yields $y = -0.556x + 1.63$, $r = -0.5562$, $P > 0.11$, two-tailed. Breeding increment thus shows a slight tendency to be negatively correlated with RSD.

*Incubation.*—In all European owls, all incubation is performed by the female. The same is almost certainly true of North American species, although it is easy to find accounts of males sharing in incubation (Bent 1938). Males may briefly cover eggs while the female leaves to defecate, preen, etc. (Glutz and Bauer 1980 list this behavior for *Otus scops, Surnia ulula,* and *Aegolius funereus*) and this may have led to the conclusion that males participate in incubation in some species. As females do all of the incubating in all species, there obviously is no correlation between RSD and the roles of the sexes in incubation behavior.

*Nest protection.*—There appears to be no relationship between RSD and which sex performs most of the defense of the nest against predators. Information on the relative role of the sexes in nest defense is available for 8 European species; in 4 the female performs more defense than the male (Eagle-, Tawny, Ural, Long-eared owls) and in 4, the male is the primary defender (Scops-, Snowy, Great Gray, Short-eared owls). A Mann-Whitney $U$-test on these data yields $U = 5$, $P = 0.243$, for RSD in weight and $U = 7$, $P = 0.443$ for wing. The evidence thus indicates no difference between the sexes in nest defense and no relationship with RSD.

*Feeding efficiency.*—Statements on which sex feeds the young are given for 10 species of European owls, including the least dimorphic, the Little

Owl, and the most dimorphic, the Great Gray Owl. There is no evidence that males tear apart prey and feed their young the pieces in any of the 10 species. There is thus no correlation between RSD and the direct feeding of young by the female.

*Foraging interference, energy conservation, and pyramid of numbers of prey sizes.*—These three hypotheses predict that the male should do most of the hunting and provision the female and brood at least until the young are quite large. Again, the information for North American owls is too limited to be useful. Provisioning of the female by the male begins in courtship and the male is the exclusive, or nearly exclusive, provider of food for the female and young through the end of the brooding phase in all European owls. Exceptions to this rule occur only when the male fails to deliver sufficient food, usually in times of prey scarcity, which occur primarily during the cyclic population "lows" of Microtine rodents. There is no evidence of a correlation between RSD and the provisioning efforts of the male.

## Behavioral Hypotheses

*Sociability.*—Only one species of North American or European owl exhibits breeding behavior that can be interpreted as colonial: the Burrowing Owl. This species' lack of RSD supports the hypothesis that coloniality inhibits the development of dimorphism. The Burrowing Owl is also known to engage in group defense against predators thus supporting the hypothesis that this reduces the "need" for dimorphism.

*Anticannibalism.*—Clear statements that the female performs all of the brooding of nestlings are given for 9 species of European owls. All brooding also appears to be done by the female in *Tyto alba, Glaucidium passerinum,* and *Athene noctua* although there is no explicit statement on the role of the sexes in these species. Possible brooding by the male is described only for *Aegolius funereus*; in this species the male has been recorded to spend much time in the nest cavity with the female during the first week after hatching and the male *may* help with brooding of the nestlings during this time. The absence of brooding by the male in the remaining 12 species suggests that there is no correlation between RSD and the participation in brooding by the male.

*Pair-bonding.* Information on dominance relationships between the sexes is available for 6 species of European owls. These are, listed in descending order of female dominance: *Glaucidium passerinum, Bubo bubo, Surnia ulula, Athene noctua, Otus scops,* and *Tyto alba.* This ranking of female dominance is significantly correlated with RSD in weight, $r_s = 0.943$; but not with RSD in wing, $r_s = 0.714$. ($P = 0.05$, at $r_s = 0.829$, and $P = 0.01$, at $r_s = 0.943$.)

Mueller and Meyer (1985) were unable to rank female dominance in species of Falconiformes and simply compared the RSD of species for which female dominance was recorded with the RSD of those for which there was no record of dominance. This method of analysis is unsuitable for the data available for owls because almost all the information is from observations of birds breeding in captivity and would thus show the relationship between captive breeding and RSD. A Mann-Whitney $U$-test on presence or absence of recorded dominance and RSD for European owls yields $U = 6$, $P = 0.017$, one-tailed for weight; and $U = 15$, $P = 0.223$, for wing; showing that dominance has been recorded significantly more often in species with low RSD in weight than in species with high RSD in weight, and suggesting that more species with low RSD have been bred in captivity than species with high RSD.

*Nest-site preference.*—Fourteen of the 19 species of North American owls prefer to nest in cavities; the remaining 5 nest in old stick nests of other birds, on cliff ledges or in open nests on the ground. A Mann-Whitney $U$-test reveals no significant relationship between RSD and nest-site preference for the 19 species (weight, $U = 17$ [for $P = 0.05$, $U = 15$]; wing, $U = 26$ [for $P = 0.05$, $U = 16$]). Seven of the 13 species of European owls prefer to nest in cavities, and the remainder breed in open nests. This sample also shows no relationship between RSD and nest-site preference (weight, $U = 13$, $P = 0.177$; wing, $U = 14$, $P = 0.217$).

## DISCUSSION

The most widely accepted hypotheses on RSD in raptorial birds all include differential use of sizes of prey by the sexes. Although most species of birds of prey show a statistically significant difference in size of the sexes, there is remarkably little evidence that the sexes take significantly different sizes of prey. The available evidence for owls indicates that female Boreal Owls take larger prey than males. However, the sample is small, the difference barely significant, and female Boreal Owls take prey that is of the same size and species composition as the much heavier (7.4×), female Great Gray Owl. The data on the Great Gray, Ural, and Boreal owls are not unique in showing great interspecific difference in size of owl but little difference in species of prey taken. Mikkola (1983) has shown that 10 species of Fenno-Scandian owls have an average similarity in diet of 0.80, using the index of community similarity of MacNaughton and Wolf (1973). This index ranges from 0 to 1, with 1 indicating complete overlap. Six of the 10 species (Snowy, Northern Hawk-, Great Gray, Long-eared, Short-eared, and Boreal owls) show a similarity index of 0.97–1.00, indicating virtual total overlap in diet. In 4 of the 6 species (Snowy, Northern Hawk-, Great Gray, Short-eared owls) the diet consists of 91.3–

97.4% Microtine rodents. The mean weights for these four species of owls range from 303 to 1983 g, a 6.5-fold difference. There is thus considerable evidence that the differences in body size of owls, either within or between species, generally result in small differences in the size of prey taken.

Although data are available from only 6 species, there is not even a suggestion of support for the prediction that trophic structures should be more dimorphic than nontrophic structures. Overall, the balance of evidence from owls is quite strongly against the ecological hypotheses of RSD.

My analyses have revealed some differences between correlations of RSD in wing measurement and weight and various other factors. I agree with Johnson (1978) that a composite index of several measures of body size and appendages acts to obscure important differences. I also agree with Earhart and Johnson (1970), Amadon (1977), and Cade (1982) in their suggestion that weight is the best measure of body size. A number of species of owls do show differences between RSD in wing and weight. Dimorphism in the cube root of weight is greater than dimorphism in wing in 21 of the 25 species. Earhart and Johnson (1970) present statistics separately for each subspecies of owl and the variance presented for weight is for the cube root. This presentation makes it difficult to establish, unequivocally, which species show statistically significant dimorphism. It appears that male Burrowing Owls have a significantly longer wing chord than females. The Flammulated, Whiskered Screech-, Ferruginous Pygmy-, Long-eared, and Short-eared owls appear to be sexually monomorphic in wing. Only the Whiskered Screech- and Burrowing owls appear to be monomorphic in weight. North American species not mentioned above appear to show significant RSD in wing or weight. Insufficient information for most European owls precludes a determination of the statistical significance of RSD; however, it appears likely that most species of owls show significant RSD in weight.

The only advantage of wing chord as a measure of body size is that it easily can be obtained from museum specimens. It is difficult to envisage any other type of animal where the most commonly used estimator of body size would be epidermal outgrowths of digits of the forelimb. The fact that the length of the longest primary does influence flight capability is not an adequate justification for widespread reliance on wing chord as the standard measure of body size. I suggest that weight is by far the best measure of body size and also that RSD in weight is of greater biological significance than RSD in wing.

Newton (1979) and Andersson and Norberg (1981) show that RSD is correlated with speed and agility of prey. Many of the invertebrates captured by owls are insects that fly at night, and owls do capture insects

in flight (e.g., Glutz and Bauer 1980). Capture of a nocturnal flying insect probably requires greater agility than capturing a nocturnal, running small mammal. If "flycatching" is important in the foraging of insectivorous owls, then agility in flight may be more important for them than for owls that specialize on small mammals. Flight performance is size-related and a bird that pursues and captures prey in flight ideally should be not much larger than its prey (Andersson and Norberg 1981). The small size, and relatively small range of sizes of insects available for capture by owls leads to the prediction that insectivorous owls should be small and show limited RSD. The range of sizes of most of the prey exploited by owls that specialize on mammals is also limited. Perhaps the limited agility required for capture not only permits a great range of sizes of species specializing on small mammals but also the evolution of considerable RSD within species. In both of the hypotheses presented above, diet permits, or limits, but does not cause RSD.

Temeles (1985) found a correlation between RSD and prey vulnerability (relative ease of capture by the predator) in the Falconiformes. Temeles' hypothesis also predicts prey-size partitioning between the sexes and species, based on body size, and thus appears to be an inadequate explanation for RSD in owls.

It is surprising to find no correlation between RSD and any of the predictions generated from the hypotheses concerning sex-role differentiation. Owls are a remarkably uniform group in the relative roles of the sexes in parental care. Females perform all incubation, brooding, and apparently all the tearing apart of prey and the direct feeding of bits of food to the young. Males perform all of the hunting and provisioning of the female and young from before the beginning of egg laying through at least the end of brooding with the exception that females will hunt if prey is so scarce that the male is unable to deliver sufficient food.

Differentiation of sexual roles in incubation, brooding, provisioning, and rearing of young occurs in a great variety of birds with "normal" dimorphism (Mueller and Meyer 1985), and it is inconsistent to argue a special case for hawks or owls except, possibly, for nest defense. There is no relationship between RSD in owls and which sex is the primary defender of the nest and young against predators. Mueller and Meyer (1985) found the same to be true for European Falconiformes. Several authors have given great importance to more efficient nest defense by large females as the deciding factor as to which sex is the larger one in raptorial birds. Snyder and Wiley (1976) emphasize that in the Burrowing Owl the male is larger than the female and is the primary nest defender. (But note that the species is monomorphic in weight.) Glutz and Bauer (1980) show that the male is the primary defender in half of the European species for which

information is available, and all of these species show RSD. More recently, Wiklund and Stigh (1983) have shown that male Snowy Owls perform almost all nest defense, and this species shows high RSD.

I have found no reasonable evidence for any of the ecological or sex-role partitioning hypotheses concerning the evolution of RSD. This leaves only the behavioral hypotheses as a possibility. Absolutely conclusive proof will be very difficult to obtain for the hypothesis that RSD facilitates the formation and maintenance of the pairbond. However, it is very important to note that female dominance is shown in species of owls with relatively low RSD, yet the degree of dominance appears to be correlated with RSD. There is no such evidence for any other hypothesis. The facilitation of female dominance is thus the most viable hypothesis on the evolution of RSD, in spite of the scarcity of data on dominance relationships. The lack of information on the breeding behavior of the more dimorphic species is also interesting. Almost all the information available on interpair relationships is from owls breeding in aviaries. Perhaps high RSD inhibits pair formation and breeding in a situation where a male cannot keep his distance and escape from an aggressive female when she is not receptive to sexual advances.

Smith (1980) lists more than 40 species of more than 20 families of birds in which the female is dominant during the breeding season. All these species are monogamous. Data are lacking for other species, but it appears likely that female dominance during the breeding season occurs in most monogamous species. All North American and European owls are monogamous, with only occasional occurrences of polygyny.

We know relatively little about the initial courtship behavior of owls. What little information we do have suggests that the female is socially dominant over the male even before the inception of courtship. Courtship behavior has been studied in detail in a variety of other monogamous birds, and the early phases almost invariably involve at least some aggression on the part of the male (Armstrong 1947, Hinde 1973). In many species the male is fully as hostile to an arriving female as to an intruding male. Smith (1982) notes that raptors possess potentially lethal weapons and suggests that RSD has evolved to facilitate female dominance. In most other species of birds, males are dominant outside of the breeding season and some aggression occurs before dominance is reversed during pair formation. Prior female dominance eliminates this potentially dangerous transition in raptorial birds.

There appears to be great reluctance to accept the idea that RSD in birds without reversal of sexual roles might be the result of sexual selection. The reluctance to accept sexual selection for RSD in raptors is apparently due to the recent concentration of work on intrasexual selec-

tion, with so little thought given to epigamic selection that it appears to be virtually forgotten. Selander (1972) has shown that it is extremely difficult to differentiate between the two types of selection. It is obvious that the female does the mate selecting in most species of birds, but it is rarely clear what influences her selection. I suggest that female raptors tend to select less dominant and aggressive males and this selection has led to the evolution of RSD.

The observed relationships between diet may be the result of prey type permitting or restricting the degree of RSD, as I have suggested. Alternatively (or also, since the hypotheses are not mutually exclusive), the rapacity of the species may be an important determinant of RSD. Species that prey upon vertebrates are certainly more rapacious than those that capture invertebrates. Perhaps the formation and maintenance of the pairbond are more difficult in formidable predators than in less rapacious species and this may be mitigated by increased RSD. Amadon (1975) has pointed out that dimorphism in size in animals, regardless of which sex is the larger, is nearly always related to mating behavior.

*Cautionary note.*—This entire paper is based on correlations, which cannot distinguish cause from effect. It is further based on the assumption that a trait important in the evolution of RSD should be expressed to a greater extent in species with high RSD than in those with low RSD. These premises are arguable, but I can see no better alternative. More work is needed on the functions and evolution of RSD in owls. We appear to have a sufficient number of hypotheses and remarkably little in the way of useful data. Further studies of RSD should concentrate on obtaining data that offer a reasonable possibility of proving or falsifying hypotheses. We particularly need observations of pair formation and other aspects of interaction between males and females, both in nature and in captivity. Further information on the diet of the sexes might be informative. Any field study on raptors should record information separately for the sexes wherever this is possible. For the present, the most viable working hypothesis appears to be that RSD evolved to facilitate female dominance which in turn facilitates formation and maintenance of the pairbond.

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# WINTER POPULATION DYNAMICS OF THREE SPECIES OF MAST-EATING BIRDS IN THE EASTERN UNITED STATES[1]

KIMBERLY G. SMITH[2]

ABSTRACT.—Winter population dynamics of Black-capped Chickadee (*Parus atricapillus*), Blue Jay (*Cyanocitta cristata*), and Red-headed Woodpecker (*Melanerpes erythrocephalus*) were examined in the eastern half of North America using National Audubon Society Christmas Count data from count areas that have had the highest number of individuals for each species in at least one winter between 1947–48 and 1983–84. All three species store and consume mast. Red-headed Woodpecker populations were most variable and Blue Jay populations were more variable than those of Black-capped Chickadees. Year-to-year comparisons show that Red-headed Woodpeckers are relatively nomadic in winter; that Blue Jays make movements between New England and the Mid-Atlantic coast with some regularity; and that Black-capped Chickadees may make relatively short population movements between central and southern New England. Movements of the 3 species were independent of mean January temperatures at the count areas examined. Results presented here are consistent with the hypothesis that increased dependence on mast as a winter food source is correlated with increased variability in winter population dynamics. In particular, the nearly periodic nature of the east–west shift of Red-headed Woodpecker high counts among years is strikingly similar to the periodic pattern of boreal seed-eating birds discovered by Bock and Lepthien (1976a). *Received 8 Oct. 1985, accepted 18 Feb. 1986.*

Most studies of birds that eat tree seeds during winter in North America have focused on species that consume conifer seeds (reviewed in Bock and Lepthien 1976a). Although a number of bird species consume mast (e.g., acorns) during fall and winter, few New World studies have examined the importance of these seeds to avian population dynamics (e.g., White and West 1977, Smith 1986). The relationship between mast production and bird abundance has received considerably more attention in Europe (e.g., Evans 1966, Perrins 1966, Erikkson 1970, Bejer and Rudeno 1985, Greig-Smith and Wilson 1985).

This study examines winter population dynamics of three common woodland birds in eastern North America: Black-capped Chickadees (*Parus atricapillus*), Blue Jays (*Cyanocitta cristata*), and Red-headed Woodpeckers (*Melanerpes erythrocephalus*). These species were chosen because they consume and cache mast crops during fall or winter (Darley-Hill and Johnson 1981, Sherry 1984, Johnson and Adkisson 1985), but differ

[1] This paper is dedicated to Frank A. Pitelka, who has long had an interest in jay and woodpecker research, on the occasion of his 70th birthday.

[2] Dept. Zoology, Univ. Arkansas, Fayetteville, Arkansas 72701.

markedly in population movements during that time. Black-capped Chickadees rarely make mass population movements (Lawrence 1958, Bagg 1969, Yunick 1981, Elder and Zimmerman 1983, Loery and Nichols 1985), Blue Jays occasionally make mass population movements (reviewed in Smith 1979a), and Red-headed Woodpeckers commonly abandon and invade areas on a yearly basis (Bock et al. 1971, Smith 1986). These differences presumably are due to the differing degrees to which these three species depend on mast as a winter food supply: Red-headed Woodpeckers completely desert areas with low acorn abundance (reviewed in Smith 1986), Blue Jays are capable of using other winter food sources (Bock and Lepthien 1976b), and Black-capped Chickadees usually depend on winter food sources other than mast crops (e.g., Forbush 1929).

I predicted that, based on dependence on mast crops, Red-headed Woodpecker winter populations would vary geographically more than those of the other two species and that Blue Jay winter populations would fluctuate more than those of Black-capped Chickadees. I also predicted that movements of these species would be independent of severe winter weather. Here I test these predictions using Christmas Bird Count data by examining those count areas that have had highest total number of individuals of the 3 species in at least one winter from 1947–48 through 1983–84. I also examine mean January temperature at each count area, a variable that T. Root (pers. comm.) has found to be a good predictor of wintering patterns of many bird species in eastern United States.

## METHODS

Data were extracted from Audubon Field Notes and American Birds for those count areas that have had the highest total number of Red-headed Woodpeckers, Blue Jays, or Black-capped Chickadees in at least one year since winter 1947–48 (see Table 1), when annual summaries of highest totals for all species reported on all Christmas Bird Counts were first reported (Stewart 1948). Although quality of CBC data vary among counts and among years (e.g., Bock and Lepthien 1974), I judged the information on these 3 species to be relatively reliable because species are common, easily identified, and conspicuous during winter.

Observer party-hours, i.e., total time in hours that parties of observers spent in the field, were also recorded for each count area. As relationships between time and bird numbers can be confounded by observer effort, which has increased greatly over the years for most counts (Smith 1979b), results of each count were divided by total observer party-hours reported to produce standardized numbers for each species (Bock and Lepthien 1974).

To determine general increases or decreases in abundance over the last 37 years, correlations were calculated between year and the highest total each year for each species. To detect local changes in abundance of each species, correlations were also calculated between year and the standardized numbers of individuals reported at each count area. Patterns in geographical variation for each species were examined by calculating correlations for standardized numbers of individuals reported each year among all count areas for a particular species. Coefficients of variation were calculated for each count area to compare variability in numbers of birds among count areas and among the 3 bird species.

## Table 1

Mean (Standard Error) and Coefficient of Variation for Black-capped Chickadee, Blue Jay, and Red-headed Woodpecker Numbers Reported at Christmas Bird Counts that had the Highest Number of Chickadees, Jays, or Woodpeckers at Least Once Since 1947 (Mean [Standard Error] of Party hours, Number of Years that a Count had the Highest Total, and [Number of Years] a Count has been Performed since 1947 are also Presented)

| Count location | Mean (SE) | CV | Mean party-hours (SE) | Number high count years (N) |
|---|---|---|---|---|
| Black-capped Chickadee | | | | |
| Concord, Massachusetts | 1697.6 (175.4) | 50.6 | 175.1 (16.1) | 16 (24) |
| Westport, Connecticut | 994.5 (61.8) | 36.6 | 143.0 (9.1) | 14 (35) |
| Cape Cod, Massachusetts | 795.1 (49.1) | 37.6 | 77.0 (3.3) | 3 (37) |
| Greenwich, Connecticut | 922.4 (100.9) | 66.5 | 155.6 (15.0) | 2 (37) |
| Hamilton, Ontario | 657.8 (53.5) | 49.5 | 169.5 (6.7) | 1 (37) |
| Blue Jay | | | | |
| Concord, Massachusetts | 1209.2 (152.5) | 61.8 | 175.1 (16.1) | 10 (24) |
| Memphis, Tennessee | 327.4 (17.5) | 32.5 | 85.8 (4.2) | 6 (37) |
| Seneca, Maryland | 733.8 (126.5) | 86.2 | 200.1 (26.4) | 4 (25) |
| Springfield, Massachusetts | 754.3 (69.4) | 49.5 | 107.9 (4.9) | 4 (29) |
| Northhampton, Massachusetts | 713.7 (75.9) | 63.8 | 153.5 (15.5) | 3 (36) |
| Nashua, New Hampshire | 466.9 (116.6) | 96.7 | 44.4 (5.0) | 2 (15) |
| Triadelphia, Maryland | 449.3 (69.4) | 92.6 | 112.3 (11.3) | 2 (36) |
| Westport, Connecticut | 515.3 (50.6) | 58.1 | 143.0 (9.1) | 2 (35) |
| Atlanta, Georgia | 363.9 (51.8) | 86.6 | 96.0 (8.0) | 1 (37) |
| Bronx, New York | 548.2 (56.0) | 62.1 | 111.3 (8.1) | 1 (37) |
| Central Suffolk County, New York | 390.7 (48.6) | 69.3 | 118.0 (8.5) | 1 (31) |
| Hartford, Connecticut | 595.4 (59.4) | 60.7 | 177.5 (15.5) | 1 (37) |
| Red-headed Woodpecker | | | | |
| Pere Marquette Park, Illinois | 108.2 (22.9) | 127.0 | 52.7 (4.3) | 6 (36) |
| Tulsa, Oklahoma | 117.6 (18.1) | 93.3 | 56.6 (4.6) | 5 (37) |
| Manhattan, Kansas | 94.5 (35.7) | 210.4 | 88.4 (14.9) | 4 (31) |
| White River N.W.R., Arkansas | 34.2 (8.4) | 131.7 | 23.1 (2.2) | 3 (29) |
| Buckeye Lake, Ohio | 52.0 (10.0) | 116.8 | 100.4 (6.1) | 2 (37) |
| Cincinnati, Ohio | 33.6 (6.5) | 118.4 | 167.1 (12.7) | 2 (37) |
| Indiana Dunes Lakeshore, Indiana | 89.9 (31.5) | 121.4 | 119.3 (9.3) | 2 (12) |
| Sullivan, Missouri | 43.8 (19.2) | 164.1 | 47.3 (6.0) | 2 (14) |
| Beverly, Illinois | 92.5 (17.4) | 80.0 | 53.7 (5.8) | 1 (18) |
| Forest Glen Preserve, Illinois | 76.3 (15.5) | 78.7 | 63.1 (4.9) | 1 (15) |
| Fort Smith, Arkansas | 26.7 (6.4) | 134.2 | 38.0 (2.7) | 1 (31) |
| Hulah Reservoir, Oklahoma | 50.9 (7.5) | 71.9 | 54.7 (2.7) | 1 (24) |
| Land Between the Lakes, Kentucky | 32.3 (9.1) | 119.8 | 38.0 (2.3) | 1 (18) |
| Mingo N.W.R., Missouri | 66.0 (16.3) | 113.0 | 26.6 (2.4) | 1 (21) |
| Montrose Lake, Missouri | 81.8 (13.1) | 71.8 | 43.9 (4.7) | 1 (20) |
| Murphysboro, Illinois | 46.3 (30.0) | 194.3 | 24.8 (2.0) | 1 (9) |
| Orchard Farms, Missouri | 44.2 (9.4) | 104.3 | 30.8 (3.2) | 1 (24) |
| Turkey Run S.P., Indiana | 45.8 (8.7) | 82.7 | 15.8 (1.5) | 1 (19) |
| Union County, Illinois | 116.6 (27.8) | 82.7 | 60.9 (7.5) | 1 (12) |

Mean January temperatures were extracted from Climatical Data (National Oceanographic and Atmospheric Administration) for the weather station closest to each count area within the United States. (All were within 25 km of count areas.) For each count area, correlations were calculated between mean January temperature and total and standardized numbers of each species.

## RESULTS

*Black-capped Chickadee population dynamics.*—The highest number of Black-capped Chickadees reported within one count area has increased steadily over the last 37 years (Spearman rho = 0.91, $P < 0.0001$), reaching a total of 3441 individuals in winter 1983–84 at Concord, Massachusetts (Fig. 1). Number of party-hours associated with the highest chickadee total also increased significantly (rho = 0.86, $P < 0.0001$), but no strong relationship existed between year and the standardized chickadee numbers (Pearson $r = -0.09$, $P = 0.59$). Thus, much of the increase in the high count of chickadees is probably due to increased observer effort.

The high total of Black-capped Chickadees during the last 36 years has been confined to 5 count areas (Table 1). (As the focus of this study is on eastern North America, the winter 1947–48 high total at Portland, Oregon, was deleted from further analysis.) The Westport, Connecticut, count had the perennial high total through the mid-1960s, but the count around Concord (started in 1960) has had 16 of the last 18 high totals. Based upon standardized numbers, Concord ($r = 0.49$, $P = 0.01$, N = 24) and Cape Cod, Massachusetts ($r = 0.33$, $P = 0.05$, N = 37) and Hamilton, Ontario ($r = 0.50$, $P = 0.002$, N = 37) all have experienced significant increases in winter chickadee sightings over the years.

Chickadee numbers in Concord were negatively correlated with those at Westport ($r = -0.41$, $P = 0.04$, N = 24), as were those on Cape Cod ($r = -0.37$, $P = 0.03$, N = 35) and at Greenwich, Connecticut ($r = -0.32$, $P = 0.05$, N = 37), suggesting significant shifts in winter abundance between central and southern New England from year to year. Chickadee numbers were positively correlated between Hamilton and Greenwich ($r = 0.38$, $P = 0.02$, N = 37).

None of the correlations between mean January temperature and total or standardized numbers of chickadees were statistically significant ($P > 0.05$) at the 4 count areas in the United States.

*Blue Jay population dynamics.*—The highest total for Blue Jays increased steadily during the period (rho = 0.86, $P < 0.0001$), peaking at 2251 individuals in winter 1981–82 at Concord (Fig. 1). Number of party-hours associated with the high total also increased significantly (rho = 0.60, $P < 0.0001$). The relationship between standardized Blue Jay numbers and year was significant ($r = 0.36$, $P = 0.03$), suggesting that Blue

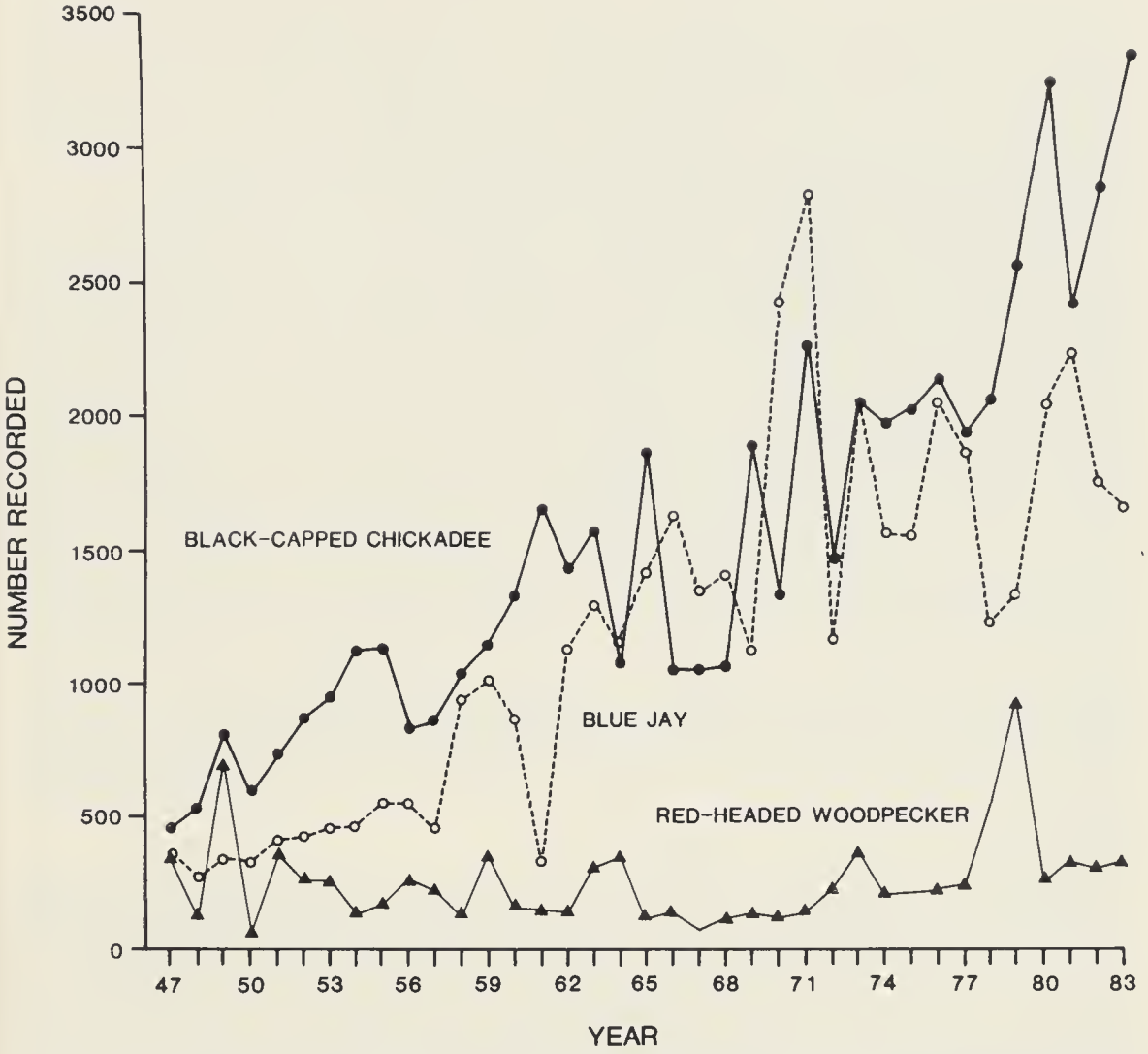


FIG. 1. Number of Red-headed Woodpeckers, Blue Jays, and Black-capped Chickadees reported on Christmas Bird Counts that had the highest number of individuals from winter 1947–48 through 1983–84.

Jay numbers have increased independently of observer effort (cf. Bock and Lepthien 1976b). Standardized jay numbers, however, were significantly correlated with year at only 2 of 12 count areas (Atlanta: $r = 0.44$, $P = 0.006$, N = 37; Seneca: $r = 0.39$, $P = 0.05$, N = 25).

Twelve count areas have had the high total number of Blue Jays at least once in the last 37 years. Four of these (33%) had the high total only once (Table 1). Jay high-count areas were more widely dispersed than were those for chickadees, and they could be classified into 4 groups based on latitude (Fig. 2A). These included southern areas (34–35°) where high counts occurred early in the history of high counts (Memphis, Atlanta), Maryland (Triadelphia, Seneca) (39°), Connecticut (Hartford, Westport) and the New York City area (Bronx, Central Suffolk County) (41°), and

central Massachusetts (Concord, Northhampton, Springfield) and southern New Hampshire (Nashua) (42–43°). Over the last 30 years, the high-count areas have been in New England, particularly Massachusetts, or in Maryland (Fig. 2A). Over the last 12 years there appears to be an approximate two-year cycle between Massachusetts and Maryland.

Examination of statistically significant correlations among count areas based on standardized jay numbers revealed a pattern that was consistent with a north–south shift in winter population dynamics of Blue Jays. In the north, numbers of jays at Concord were positively correlated with those at Northhampton ($r = 0.43$, $P = 0.05$, N = 21), Springfield ($r = 0.42$, $P = 0.04$, N = 24), and Bronx ($r = 0.48$, $P = 0.02$, N = 24); numbers at Springfield were positively correlated with those at Northhampton ($r = 0.42$, $P = 0.05$, N = 22), Hartford ($r = 0.68$, $P < 0.0001$, N = 29), Westport ($r = 0.55$, $P = 0.002$, N = 29), and Bronx ($r = 0.37$, $P = 0.05$, N = 29); numbers at Northhampton were positively correlated with those at Bronx ($r = 0.54$, $P = 0.009$, N = 22), as were those at Hartford and Westport ($r = 0.65$, $P < 0.0001$, N = 35). In the south, jay numbers at Seneca were positively correlated with those at Triadelphia ($r = 0.41$, $P = 0.04$, N = 25) and Atlanta ($r = 0.45$, $P = 0.02$, N = 25). The only significant negative correlation among all count areas was between Westport and Atlanta ($r = -0.34$, $P = 0.05$, N = 35).

Significant correlations between jay numbers at Memphis with those at Concord ($r = 0.47$, $P = 0.02$, N = 24), Northhampton ($r = 0.44$, $P = 0.04$, N = 22), Springfield ($r = 0.63$, $P = 0.0002$, N = 29), Hartford ($r = 0.44$, $P = 0.007$, N = 37), and Westport ($r = 0.34$, $P = 0.05$, N = 35) are inconsistent with the pattern mentioned above. The reason for these relationships remains obscure, particularly as jay numbers (and party-hours) have remained relatively constant at Memphis, while varying considerably at the other sites (Table 1).

Mean January temperatures and jay numbers were negatively correlated at Northhampton (rho = $-0.45$, $P = 0.007$, N = 34), Hartford (rho = $-0.33$, $P = 0.05$, N = 36), and Atlanta (rho = $-0.40$, $P = 0.01$, N = 36). The relationships at the two Maryland count areas were close to being significant (Triadelphia: rho = $-0.33$, $P = 0.06$, N = 34; Seneca: rho = $-0.36$, $P = 0.08$, N = 24), suggesting that more jays were observed in more southerly areas during cold winters there. All of these relationships may be due to increased observer effort as no correlations between standardized jay numbers and temperature were statistically significant at any count area, although the correlation for the Atlanta count was close to significance ($r = -0.31$, $P = 0.06$).

*Red-headed Woodpecker population dynamics.*—In contrast to the other species studied, the high total for Red-headed Woodpeckers has not

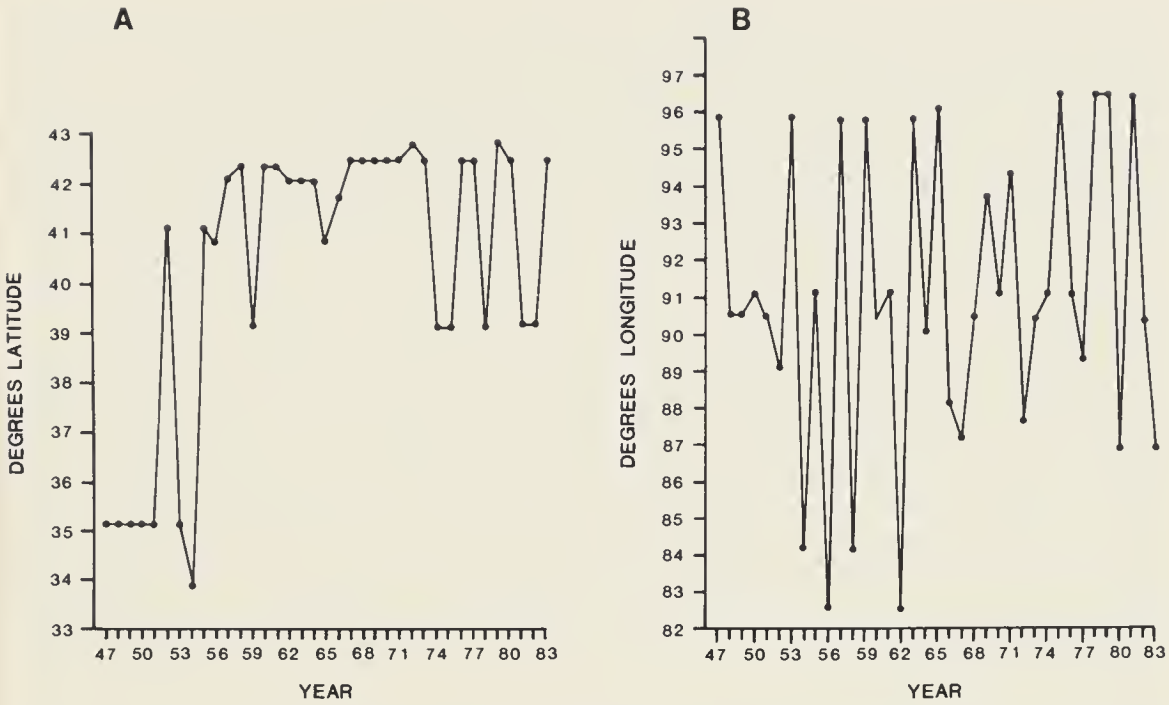


FIG. 2. Latitude of count area with the highest number of Blue Jays (A) and longitude of the count area with highest number of Red-headed Woodpeckers (B) from winter 1947–48 through 1983–84.

increased significantly over the last 37 years (rho = 0.16, $P = 0.33$). The highest number reported was 914 individuals at Manhattan, Kansas, in winter 1979–80 (Fig. 1). There was also an "estimate" of 700 woodpeckers associated with pecan groves around the Pere Marquette Park count in winter 1949–50 (Anonymous 1952). Party-hours associated with the high woodpecker number have continued to increase significantly (rho = 0.42, $P = 0.01$), meaning that more observer effort has produced relatively fewer woodpeckers ($r = -0.35$, $P = 0.04$).

During the last 37 years, 19 Christmas Bird Count areas had the high count for Red-headed Woodpeckers; 11 of these (58%) had the high total only once (Table 1). These count areas are more widely dispersed than those of the previous 2 species, and they can be classified into 4 groups based on longitude (Fig. 2B). These include Ohio (Cincinnati, Buckeye Lake) (82–85°); Indiana (Indiana Dunes, Turkey Run), Kentucky (Land Between Lakes), eastern Illinois (Forest Glen Preserve) (87–88°); western Illinois (Murphysboro, Beverly, Pere Marquette), eastern Missouri (Orchard Farms, Mingo National Wildlife Refuge, Sullivan), eastern Arkansas (White River National Wildlife Refuge) (89–91°); and western Missouri (Montrose Lake), western Arkansas (Fort Smith), Oklahoma (Tulsa, Hulah Reservoir), Kansas (Manhattan) (94–96°). Year-to-year geographic variation in these areas was great. For example, for each year that the

high total was in Ohio, the high total either the preceding or succeeding year was in Tulsa (Fig. 2B). No obvious long-term trends in woodpecker occurrence were evident from examination of the location of individual count areas. For example, the Pere Marquette Park count had the high total during winters 1948–49, 1949–50, 1951–52, 1968–69, 1973–74, and 1982–83. Also, unlike the other two species, it was unusual for the high total to be at the same count area for two consecutive years (two instances) (Fig. 2B).

Although it appears difficult to predict where the high count for Red-headed Woodpecker will occur in any given year, nearly half the high totals have occurred near the center of the wintering range (e.g., Peterson 1980). About a fourth of the high totals have occurred with regularity over the last 37 years along the extreme western edge of the wintering range, formerly in Oklahoma and more recently in Kansas. The high total area formerly was found as far east as Ohio, but recently it has not been farther east than Indiana.

Unlike the other two species, no geographic pattern was evident in the statistically significant correlations among count areas based on standardized woodpecker numbers. Only 13 of the 171 pair-wise comparisons (7.6%) between the 19 high count areas were significant ($P < 0.05$), which is not much higher than predicted by chance alone.

No correlations between mean January temperature and woodpecker numbers were statistically significant. Only one of the 19 comparisons between temperature and standardized numbers was statistically significant (Fort Smith: $r = 0.41$, $P = 0.02$, N = 30), which is the number expected by chance alone.

*Comparisons among the three species.*—The high annual totals for Black-capped Chickadees and Blue Jays were significantly correlated (rho = 0.74, $P < 0.0001$, N = 36). This relationship disappeared, however, when standardized numbers were analyzed ($r = -0.04$, $P = 0.81$, N = 34), suggesting that increased observer effort was the underlying cause of the relationship. Red-headed Woodpecker annual high totals were not significantly correlated with those for either chickadees or jays in any analysis.

Red-headed Woodpecker winter populations fluctuated to a greater degree than those of chickadees or jays (Table 1). Blue Jay and Black-capped Chickadee populations had similar magnitudes of fluctuation in New England, but jay populations in Maryland and at Atlanta were relatively more variable than those further north.

## DISCUSSION

Results presented here are consistent with the hypothesis that greater dependence on mast crops as a winter food source is associated with

greater spatial and temporal variation in abundance during winter. Numbers of Red-headed Woodpeckers, the species most reliant on mast crops, were more variable than those of the other two species in all aspects of wintering population dynamics examined. Fluctuations in jay numbers were intermediate between those of woodpeckers and chickadees. Severe winter weather (based on mean January temperature) did not appear to influence the population dynamics of these species.

The relatively large number of count areas that have had the high total of Red-headed Woodpeckers supports the suggestion by Bock et al. (1971) that Red-headed Woodpeckers seek out areas with high mast abundance. For example, the Pere Marquette Park count has had the high total more than other counts presumably due to woodpeckers being attracted to the pecan groves near the count area. Manhattan has had the high count several times in recent years because participants in the count devote more attention to the riparian oak woodlands on the Konza Prairie, areas within the census circle that were neglected in years past (C. C. Smith, pers. comm.). But even at these two areas, there were years when no Red-headed Woodpeckers were reported. In some respects, the winter population fluctuations of Red-headed Woodpeckers are similar to those of nomadic carduline finches (e.g., crossbills) that search for and are attracted to areas with high coniferous cone crops (Smith 1978). A high count of Red-headed Woodpeckers one year is no guarantee that any woodpeckers will be present the following year in the same area.

The relative consistency with which the high count for Red-headed Woodpeckers occurs on the extreme western edge of the wintering range is of interest. Although the origin of birds appearing in these areas is unknown at present, it is tempting to speculate that these birds are coming from the breeding areas to the west and north of the wintering range, stopping in years when mast crops are abundant, but continuing eastward when mast crops are low. Fall mast crop surveys conducted by Christisen (1980) in Missouri from 1954 through 1980 lend support to this theory. During those 27 years, only two years (1964 and 1970) were classified by Christisen as "good" mast crop years, the other 25 years being classified as "fair." In both those good years, the count area with the highest number of Red-headed Woodpeckers was in Missouri (Mingo National Wildlife Refuge and Sullivan, respectively).

Unlike Red-headed Woodpeckers, Blue Jays almost never completely abandon wintering areas; rather, populations fluctuate between high and low years (Smith 1986). Nonetheless, in areas where these species co-occur in winter, such as the Ozarks, populations of both species closely co-vary, which Smith (1986) attributed to use of mast crops by both species. Results presented here suggest that in some years populations of Blue Jays in the east move down the coast from New England to Maryland,

presumably corresponding to food shortages in the north. Such a migratory pattern for Blue Jays is well-documented by banding recovery data (e.g., Kennard 1980, Stewart 1982). These results are also consistent with the claim that Blue Jays in general appear to be wintering further north now than they have in the past (Bock and Lepthien 1976b; T. Root, pers. comm.).

Winter populations of Black-capped Chickadees also experienced high and low years (Loery and Nichols 1985). Several researchers (Perrins 1966, Bejer and Rudeno 1985) have linked mast crop abundance with population density in several species of European parids. Bagg (1969) demonstrated that movement of primarily juvenile chickadees in Maine and Ontario was correlated with low levels of both conifer and mast crops. Results presented here suggest some coordination between population levels in Massachusetts and the Connecticut coast. Chickadee populations may move between central and southern New England (see Lawrence 1958), but, at present, most data suggest shorter winter movements for Black-capped Chickadees in Massachusetts (Smith 1984). Also, based on the last 18 years, one might expect the high total for Black-capped Chickadees to occur at Concord nearly every year.

The nearly cyclic east–west pattern found in the occurrence of the Red-headed Woodpecker high counts (Fig. 2B) strikingly parallels the north–south eruptive pattern of seed-eating boreal birds discovered by Bock and Lepthien (1976a). By combining a variety of data sets on seed abundance, these researchers were able to demonstrate that southern movements were correlated with a general circumboreal seed crop failure. While comparable data for mast abundance throughout the eastern United States are lacking, mast abundance may be the underlying factor responsible for the geographic pattern in Red-headed Woodpecker high counts. A cyclic north–south pattern also emerges in the occurrence of Blue Jay high counts (Fig. 2A).

## ACKNOWLEDGMENTS

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## NORTH AMERICAN LOON FUND GRANTS

The North American Loon Fund (NALF) announces the availability of two grant programs for support of new or current research, management, or education projects that may yield useful information for Common Loon conservation in North America.

The first of these programs, the Robert J. Lurtsema Research Award, consists of a $1,000 stipend available annually for a suitable research project focused on a member of the Family Gaviidae. Preference will be given to students and independent researchers with limited availability of other funding.

The second program offers modest grants in support of research, management, or educational projects directly related to the conservation of Common Loons as a breeding species. Proposals in the range of $500 to $3,000 are most likely to be considered for funding.

Further guidelines for prospective applicants are available upon request from the NALF Grants Committee. Deadline for submission of proposals is January 31, 1987. Funding awards will be announced by March 15th.

Please submit guideline requests to:

North American Loon Fund Grants Committee
North American Loon Fund
Main St., Meredith, NH 03253

*Wilson Bull.*, 98(3), 1986, pp. 419–432

# SOCIAL ORGANIZATION, MOVEMENTS, AND HOME RANGES OF BLUE GROUSE IN FALL AND WINTER

JAMES E. HINES[1]

ABSTRACT.—Social organization, movements, and home ranges of Blue Grouse (*Dendragapus obscurus*) were investigated on Hardwicke Island, British Columbia from 1979 to 1982. Most broods disbanded by the end of September, and young grouse did not associate with their mothers or siblings in winter. The tendency to form flocks was lowest in fall. Grouping increased gradually until midwinter and then declined until spring. Approximately half of the grouse observed during winter were in groups that usually consisted of 2 or 3 birds ($\bar{x}$ = 2.9 ± 0.1 [SE], N = 210). Daily movements were usually small during winter (median = 69 m) and home ranges averaged 16.8 ± 2.3 ha (N = 21). Although Blue Grouse did not show the strong segregation of sexes found in some other tetraonines, birds most frequently associated with individuals of their own sex and age. The partial segregation of grouse by sex and age may have resulted because females wintered at lower elevations than males and juveniles migrated longer distances than adults. Segregation of sexes of other species of grouse may be explained by a similar mechanism. Flock formation is most frequent in species of grouse that winter in open areas and less frequent in species that winter in forests. *Received 20 Sept. 1985, accepted 18 Feb. 1986.*

Studies of the social organization of grouse and other birds have usually emphasized the breeding season, with mating systems drawing particular attention (Wiley 1974, Wittenberger 1978, Oring 1982). The nonbreeding season is thought to be a critical period for mortality in avian populations (Lack 1954, 1966; Bendell 1972; Fretwell 1972), and selective pressures during fall and winter may be important in shaping the overall patterns of avian sociality.

During winter, many species of grouse tend to form single sex flocks. A possible proximate explanation for this segregation is that the sexes migrate different distances or prefer different kinds of habitats and hence are not in contact with each other during winter (Koskimies 1957, Weeden 1964, Irving et al. 1967, Hoffman and Braun 1977, and others). Other possibilities are that males and females avoid each other or that members of the same sex are attracted to each other (de Vos 1983). The relative importance of any of these factors in determining the fall and winter sociality of grouse has received little attention, as winter studies are seldom undertaken and it is difficulty to identify different sex and age classes in the field.

From 1979 through 1982, I studied Blue Grouse (*Dendragapus obscu-*

[1] Dept. Zoology, Univ. Alberta, Edmonton, Alberta T6G 2E9, Canada. (Present address: Wildlife Management Division, Dept. Renewable Resources, Yellowknife, Northwest Territories X1A 2L9, Canada.)

*rus*) wintering on Hardwicke Island, British Columbia, Canada. Here, I describe groupings, movements, and home ranges of grouse during fall and winter. These data are then compared with those for other grouse in an attempt to identify (1) ecological conditions that lead to flocking and (2) factors that influence segregation of the sexes during winter.

## STUDY AREA AND METHODS

Hardwicke Island (50°28′N, 125°50′W) is in the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). Much of the 77-km$^2$ island has been logged or burned in the past 100 years and has a variety of successional stages. Breeding densities of coastal Blue Grouse reach peak numbers in openings created by logging or fire, but plant succession occurs rapidly in such openings and, about 20 years after disturbance, dense coniferous cover again prevails, herbaceous cover decreases, and numbers of Blue Grouse decline (Zwickel and Bendell 1972, Niederleitner 1982). On Hardwicke Island, most Blue Grouse wintered in early seral stages or mature forest and generally avoided dense, second-growth forests (Hines 1986).

General methods used in studies of coastal Blue Grouse were described by Zwickel and Bendell (1967a) and Zwickel (1982). From late April until late August, a 464-ha study area consisting mainly of early successional stages (<15 years in age) was searched by census crews consisting of 2 or 3 people. Grouse were located with pointing dogs, captured with noosing poles (Zwickel and Bendell 1967b), and individually marked with colored legbands. In late summer and fall 1979–81, 235 juvenile grouse were equipped with radio packages similar to those described by Brander (1968). Most marked grouse observed in the present study were captured originally on the breeding range.

Fall and winter field work was conducted over much of the island from 1 September until 31 March in 1979–80 and 1981–82 and from 1 September until 12 December in 1980. Radio-marked grouse were located with a portable receiver and yagi antenna; grouse without radios were found with a pointing dog. For many sightings of both radioed and nonradioed grouse, the surrounding area was searched thoroughly with a dog to determine if other grouse were present. Grouse found in tall trees or without the aid of a dog were omitted from analyses of fall and winter groupings as the presence or absence of other birds usually could not be determined under these conditions.

A bird was considered alone if no other grouse was found within a 10-m radius. Although this criterion was somewhat arbitrary, increasing the distance to 50 m would not appreciably change the results as grouse were seldom found within 11–50 m of each other. I believe the definition was appropriate because visibility in winter habitat was usually restricted to distances of 10 m or less and I found no evidence that grouse communicated vocally over long distances. Sightings of 2 or more individuals were said to be "flocks," "groups," or "aggregations." Although these terms are used interchangeably, it is not certain if the groups were true flocks in the sense of being cohesive social units. Given the relatively low densities of grouse on winter range, however, the probability of finding 2 birds within 10 m of each other was exceedingly low and "flocks" were probably more than coincidental or random associations.

In winter, the sex of Blue Grouse was readily determined in the field as males and females differ markedly in size and plumage. The body size and plumage of a juvenile is similar to that of an older bird of the same sex, and age could be determined only when a grouse was captured or identified by colored legbands. Grouse were classified as juveniles (i.e., hatched in the previous summer; <11 months in age) or adults (i.e., all older birds). Sample sizes were not sufficient to allow subdivision of the data into adult and yearling categories.

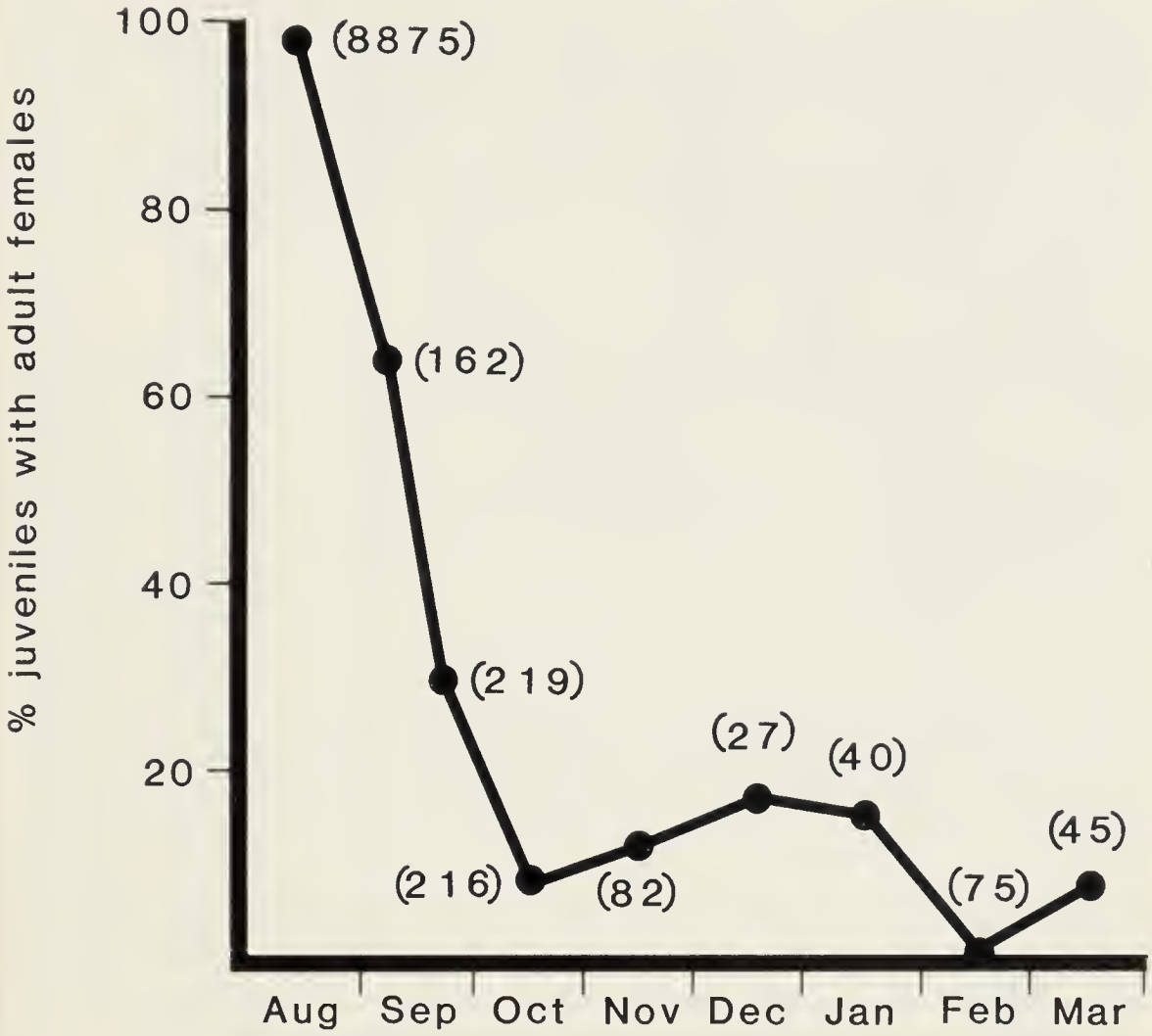


FIG. 1. The proportion of juvenile Blue Grouse observed with adult females during fall and winter on Hardwicke Island, British Columbia. Sample sizes are in parentheses.

When juveniles were individually identified during fall and winter, I attempted to determine if they were with their mothers or siblings. For this purpose, the probable mother of a juvenile was defined as the female with which the juvenile was first sighted in summer. Juveniles having the same probable mother were treated as siblings.

Minimum daily movements and home range sizes of radio-tagged grouse were measured. Daily movement was defined as the straight-line distance between the location of an individual on one day and its location on the following day. Home range size, the total area used by an animal during winter, was determined by the minimum area method (Mohr 1947) for grouse that had settled on winter range and were located 10 or more times after 1 November (but before the time they migrated in spring).

Statistical analyses involved comparisons of frequencies with contingency tables followed by pairwise contrasts (Brown 1974) when the overall $\chi^2$ value was significant ($P < 0.05$).

## RESULTS

*Brood break-up.*—Virtually all juveniles sighted in July and early August were in broods associated with older females. By late August, some

broods had started to disband, and by the end of September most juveniles had separated from adult females (Fig. 1). Because of brood break-up, only a small sample of juveniles whose mothers were known were found together in fall and winter. In September, 49% of these juveniles were found with siblings (N = 49). After 1 October, no juveniles were found with either brothers or sisters (N = 73). Thus, brood break-up likely was completed by 1 October.

*Formation of fall and winter flocks.*—The tendency for grouse to aggregate decreased throughout fall and was low in November for both males and females (Fig. 2). The decline in flocking was likely a function of brood break-up. After November, flocking again increased and peaked in January and February. In late February–early March, the number of grouse in flocks declined as older males returned to breeding areas. For example, 54% of 406 males were found in aggregations between 1 October and 1 March but only 18% of 160 males sighted in March were in groups ($P < 0.01$). In April, 22% of the males (N = 373) and 36% of the females (N = 148) observed during census of the main study area, were with other grouse. The latter figure likely overestimated the proportion of females in groups because the census crew concentrated on territorial males early in spring, and many of the females recorded were with these territorial males. In April 1982, I intensively searched a 50-ha plot as part of a study of movements and spatial relationships of female grouse and found 10 of 57 females (18%) with other grouse. This is probably a better indicator of the gregariousness of females during April.

Seasonal trends in flock size followed a pattern similar to the above data (Fig. 2). Flocks were relatively small in November but increased in size until January and then declined. Flocks sighted after brood break-up (i.e., after 1 October) consisted of 2–15 birds and averaged 2.9 ± 0.1 [SE] (N = 210). Two was the most common group size (Fig. 3).

The tendency to join flocks varied somewhat among sex and age classes. From 1 October (after the end of brood break-up) until the time of spring migration (beginning approximately 1 March for males, and 1 April for females), 46% of 127 adult males, 38% of 112 adult females, 57% of 170 juvenile males, and 55% of 267 juvenile females were found in groups. The proportion of grouse found in groups differed significantly among sex and age classes ($P < 0.01$); the only significant pairwise comparison ($P < 0.05$) indicated that adult females were less apt to be found in groups than were juvenile males or females.

Overall, 54% of the males (N = 406) and 51% of the females (N = 495) observed between the time of brood break-up and spring migration were in groups. (Grouse of known sex but unknown age were also included in these samples.) If data for both sexes were pooled, and sightings of birds

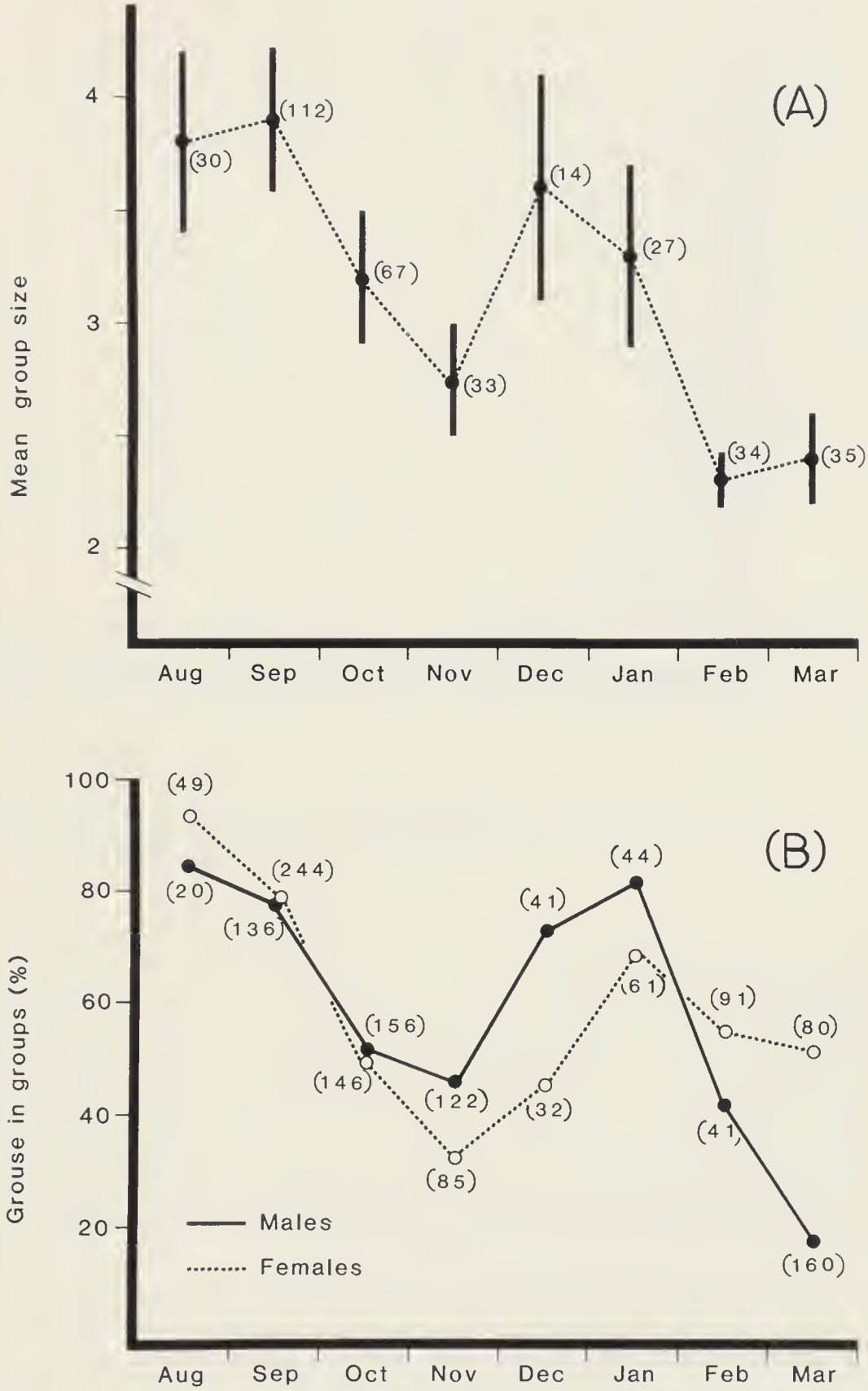


FIG. 2. The average size ±SE of flocks during fall and winter (A) and the proportion of all grouse found in flocks (B).

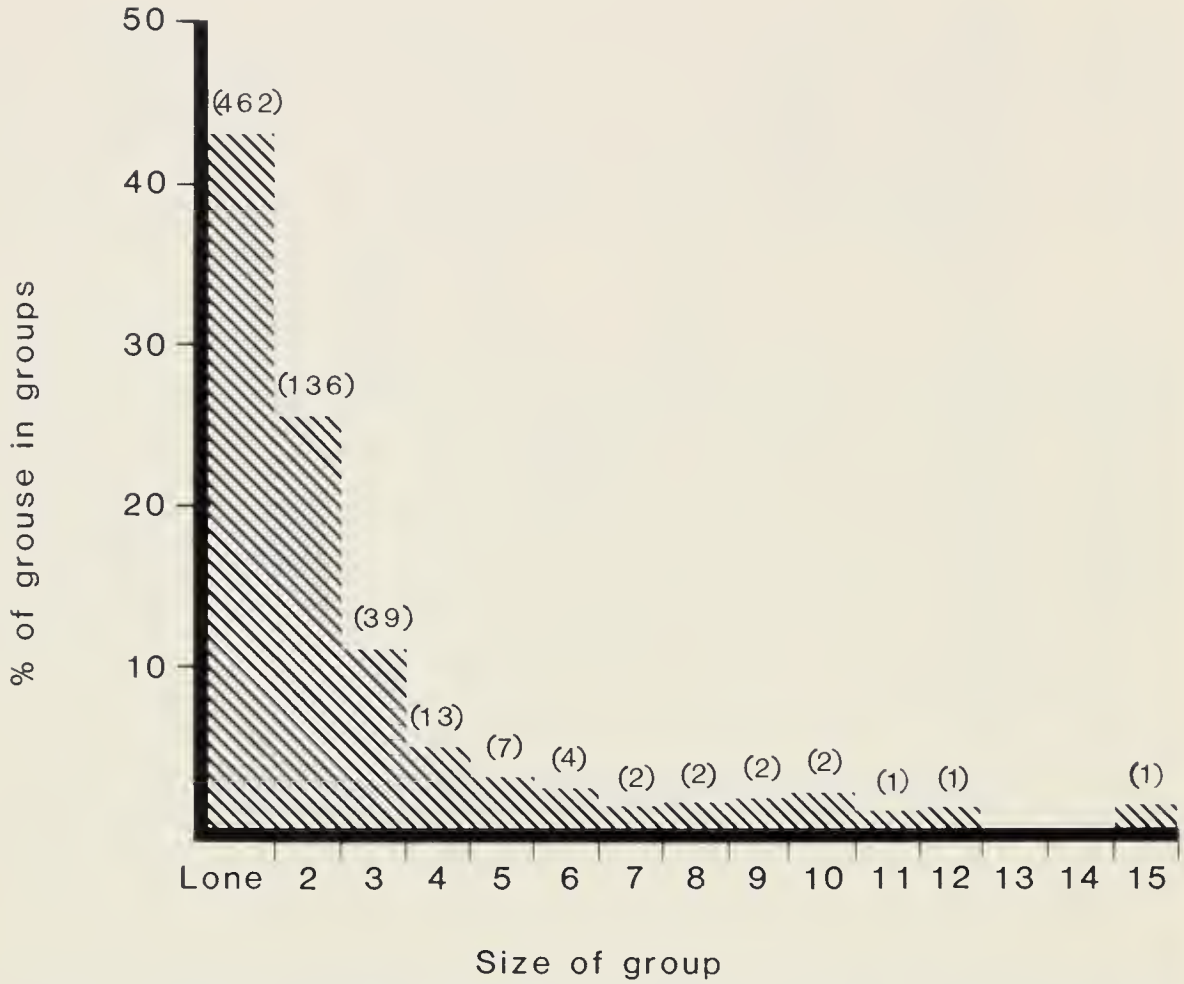


FIG. 3. Frequency distribution of flock sizes of Blue Grouse between 1 October and the time of spring migration. The number of flocks of each size are indicated in parentheses.

of unknown sex added to the sample, an estimated 52% of the grouse were in groups (N = 1029).

*Associations among different sex and age classes.*—Grouse associated most frequently with individuals of their own sex and age class, although some degree of association among all sex and age classes was found. For example, 68% of all adult males found in groups were associated with at least one other adult male, whereas only 15% were associated with adult females, 24% with juvenile males, and 9% with juvenile females (Table 1). Adult females flocked less with members of their own sex and age then did any of the other sex and age classes.

*Daily movements and home range size.*—Daily movements of radio-marked grouse were greatest in late summer and decreased during fall; they remained low but stable throughout winter (Fig. 4). Daily movements varied from 0 to over 600 m, but the median for the period lasting from 1 October until spring migration was only 69 m, indicating that short daily movements were typical (Fig. 5).

TABLE 1

ASSOCIATIONS BETWEEN BLUE GROUSE OF DIFFERENT SEX AND AGE ON HARDWICKE ISLAND, 1 OCTOBER TO 31 MARCH (DATA INCLUDE ONLY GROUSE SEEN IN FLOCKS)

| | | | % in flocks with | | | |
|---|---|---|---|---|---|---|
| Age | Sex | (N) | Adult males | Adult females | Juvenile males | Juvenile females |
| Adult | Males | 66 | 68.2 | 15.2 | 24.2 | 9.1 |
| Adult | Females | 43 | 23.3 | 23.3 | 18.6 | 30.2 |
| Juvenile | Males | 98 | 15.3 | 16.3 | 73.5 | 50.0 |
| Juvenile | Females | 148 | 6.8 | 12.2 | 28.4 | 73.7 |
| | | | Males | | Females | |
| All males[a] | | 247 | 80.6 | | 53.4 | |
| All females[a] | | 251 | 41.0 | | 76.1 | |

[a] Analysis includes 83 males and 60 females of unknown age.

Sizes of winter home ranges were determined for 18 radio-tagged juvenile females, 2 juvenile males, and 1 adult female. Home ranges during winter varied in size from 3.0 to 42.5 ha and averaged 16.8 ± 2.3 ha (N = 21). In many instances, overlap of home ranges was substantial (Fig. 6). Only radio-marked grouse on part of the island are shown in Fig. 6 and, as many other grouse resided in this area, home range overlap was undoubtedly more extensive than indicated.

## DISCUSSION

Winter was a time of relatively low mobility for Blue Grouse on Hardwicke Island. Daily movements of <100 m were most frequent, and home ranges averaged 16.8 ha for a 4–5 month period. Grouse were most often found alone or in small groups of 2 or 3 in late fall and winter, and the data suggest that winter associations of juveniles were comprised of non-siblings.

Immediately after brood break-up, the tendency to form flocks was low, but rates of aggregation gradually increased until midwinter then declined until spring. The cause of increased flocking in midwinter is not certain; it may reflect the concentration of birds in areas of suitable habitat or increased sociability. Similar trends in winter flocking occur in Ruffed Grouse (*Bonasa umbellus*) (Doerr et al. 1974), Black Grouse (*Tetrao tetrix*) (Hanson and Soikkeli 1984), and Capercaillie (*Tetrao urogallus*) (Pulliainen 1981). Doerr et al. (1974) suggested that decreases in feeding aggregations of Ruffed Grouse from January through March occurred when males became socially intolerant of each other and more attached

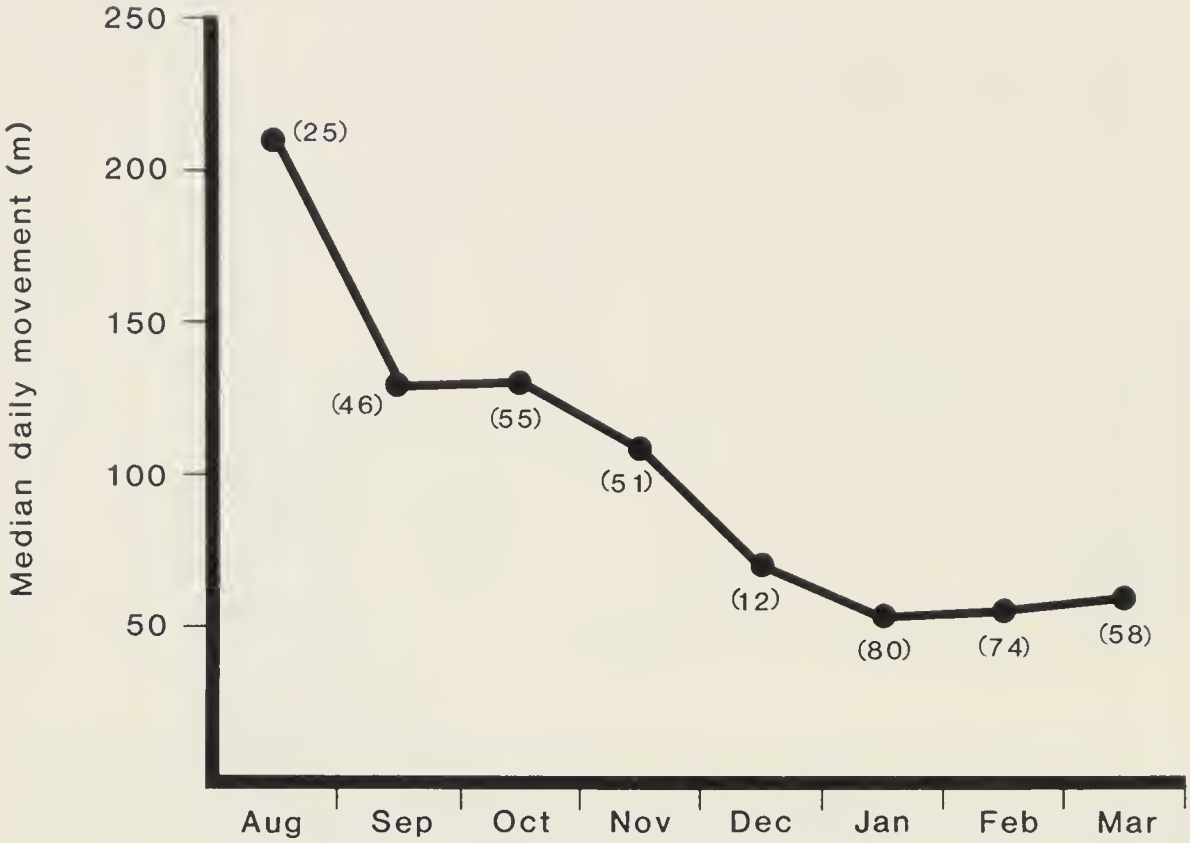


FIG. 4. Seasonal changes in daily movements (m) of radio-marked grouse. Sample sizes are in parentheses.

to their territories. This was likely true for Blue Grouse on Hardwicke Island as well, because there were proportionally fewer males in late winter flocks than in earlier groupings. Final dissolution of winter flocks occurred when females returned to breeding range.

Although Blue Grouse associated most frequently with individuals of their own sex and age, they did not show as strong a tendency to segregate by sex as do some other species of grouse. Data from studies of migration and winter habitat use by Blue Grouse (Hines 1986) suggest 2 factors that may have contributed to the partial segregation of grouse by sex and age. First, females wintered at lower elevations than males and the 2 sexes were separated somewhat because of this. Second, juveniles wintered farther from breeding range than adults, thereby bringing about partial segregation of the age classes. Given that both migration distances and the elevations at which the different sex and age classes wintered were somewhat variable (Hines 1986), the segregation of sex and age classes was incomplete. Data for other species of North American grouse support the view that segregation of the sexes is influenced by migration (Table 2). Segregation occurs most frequently when one sex winters closer to the breeding range (e.g., Sage Grouse [*Centrocercus urophasianus*], White-

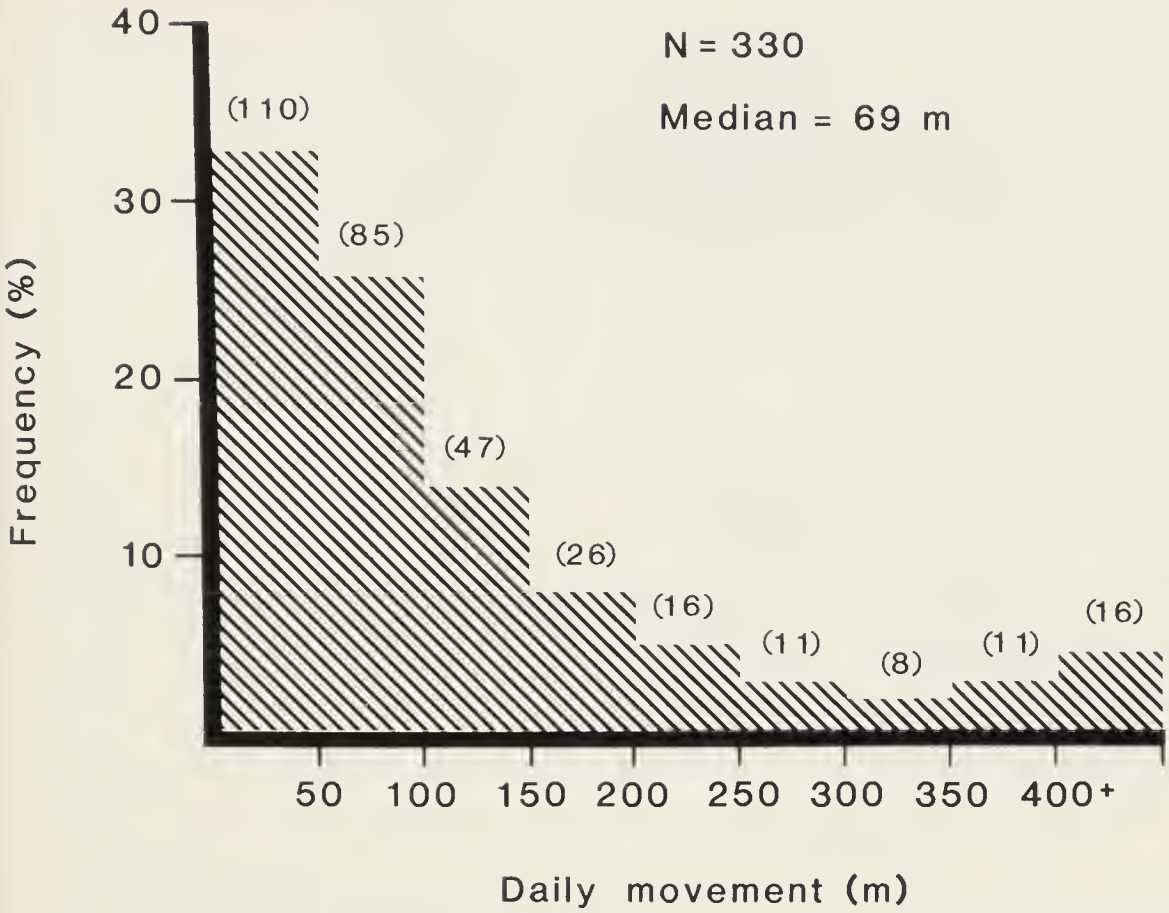


FIG. 5. Frequency distribution of daily movements (m) of radio-marked Blue Grouse during fall and winter. Sample sizes are indicated above the histogram.

tailed Ptarmigan [*Lagopus leucurus*], Sharp-tailed Grouse [*Tympanuchus phasianellus*]), and formation of mixed flocks is more common in species that show little evidence of differential migration of the sexes (e.g., Blue Grouse on Hardwicke Island, Spruce Grouse [*D. canadensis*] in Alaska, Ruffed Grouse).

The question of why certain sex and age classes associate with each other was considered above, but this does not explain why there is such a range in gregariousness among species. To address the latter question, data on fall and winter groupings of Blue Grouse and other North American Tetraoninae were summarized with regard to typical and maximum flock size and winter habitat (Table 2). Although not all information was available for each species, species wintering in more open habitats seem to form large flocks (e.g., Sage Grouse, White-tailed Ptarmigan, Sharp-tailed Grouse), whereas species wintering in forested areas live solitarily or in small flocks (e.g., Ruffed Grouse, Blue Grouse, Spruce Grouse).

There are at least three ultimate or evolutionary pressures on animals to live in groups outside the breeding season (Alexander 1974, Wilson

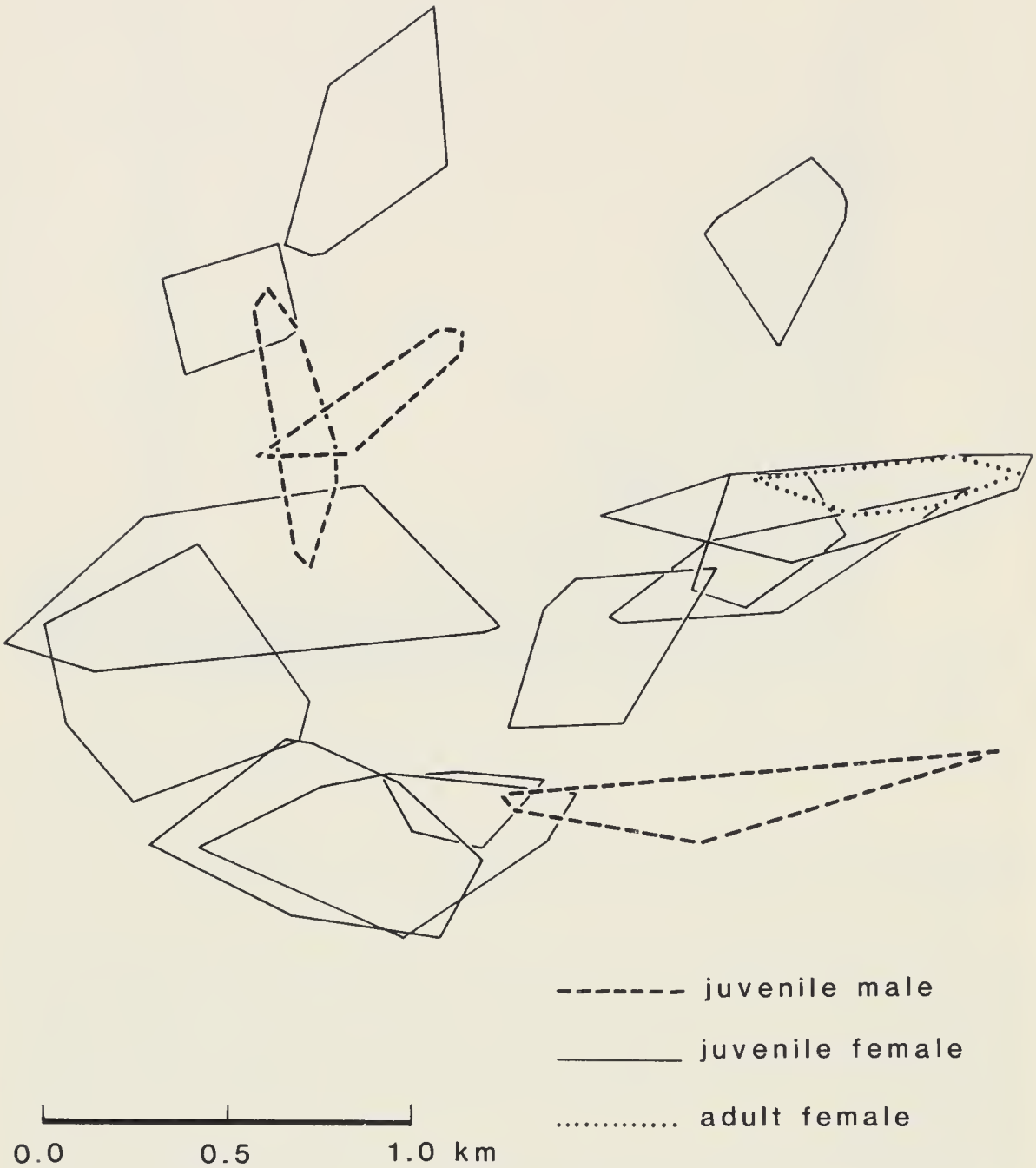


FIG. 6. Overlap of home ranges of 16 radio-marked Blue Grouse on part of Hardwicke Island, British Columbia during the winter of 1981–82.

1975, Pulliam and Millikan 1982, Madison 1984). By joining a group, an individual may (1) increase its chance of avoiding predators or (2) find and exploit a food resource more efficiently. In addition, individuals may aggregate in certain areas because (3) resources essential for survival are clumped in distribution and are not easily defended (Pulliam and Millikan 1982). The literature on grouse provides little information bearing on point (3)—it is not known if essential resources are more clumped in open

TABLE 2

FACTORS ASSOCIATED WITH FALL AND WINTER FLOCKING OF NORTH AMERICAN GROUSE

| Species | Location | Lone grouse | Typical flock size | Maximum flock size | Segregation of sexes | Winter habitat | Differential migration | Source |
|---|---|---|---|---|---|---|---|---|
| Sage Grouse | Colorado | Infrequent | <50 | 100+ | Yes | Sagebrush-grassland | Yes | Beck (1977) |
| Sage Grouse | Idaho | | <50 | 300 | Yes | Sagebrush | | Dalke et al. (1963) |
| White-tailed Ptarmigan | Colorado | Infrequent | <25 | 80+ | Yes | Alpine willow | Yes | Hoffman and Braun (1975, 1977) |
| Willow Ptarmigan | Alaska | Infrequent | | | Yes | Willow | Yes | Weeden (1964), Irving et al. (1967) |
| Rock Ptarmigan | Alaska | Infrequent | <20 | 100 | Yes | Willow | Yes | Weeden (1964) |
| Spruce Grouse | Alaska | Frequent | 2–4 | 15 | No | Coniferous forest | No? | Ellison (1973) |
| Sharp-tailed Grouse | Saskatchewan | | 5–10 | | Yes | Aspen parkland | Yes | Schmidt (1980) |
| Sharp-tailed Grouse | Wisconsin | | | 200 | Yes | Brushy areas | Yes | Hamerstrom and Hamerstrom (1951) |
| Blue Grouse | British Columbia | Frequent | 2 | 4 | Yes | Coniferous forest | Yes | King (1971) |
| Blue Grouse | British Columbia | Frequent | 2–3 | 15 | Moderate | Coniferous forest | No | This study |
| Ruffed Grouse | Alberta | Frequent | 2–3 | 9 | No | Aspen forest | No? | Doerr et al. (1974) |
| Ruffed Grouse | Saskatchewan | Frequent | 2 | 8 | | Deciduous forest | | Hines (1984) |

than forested areas. Instances of starvation seldom have been reported for grouse (e.g., McGowan 1969), suggesting that the need to exploit a food resource optimally is not the cause of tetraonine sociality. Predation, however, is a frequent cause of death for grouse (Jenkins et al. 1964, Gullion and Marshall 1968, Rusch and Keith 1971). Thus, flocking may be an antipredator response used by grouse inhabiting open areas. Comparisons of the distribution and abundance of resources, and assessments of the relative merits of flocking for maximizing feeding or avoiding predators in open vs forested habitats, and interactions among these variables are needed to resolve this issue.

## ACKNOWLEDGMENTS

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# SUBSPECIES OF THE GREATER SCAUP AND THEIR NAMES[1]

RICHARD C. BANKS[2]

ABSTRACT.—The name *Fuligula mariloides* Vigors, presently used by many authors for a subspecies of the Greater Scaup, *Aythya marila,* was originally proposed for the Lesser Scaup, *A. affinis,* and may not be used in combination with the name *marila.* The name *mariloides* has been applied to a population of Greater Scaup in Kamchatka and the Commander Islands, supposedly distinguished by small size and dark dorsal color, or for that population and the one in North America, otherwise known as *A. m. nearctica.* Evidence for a subspecifically distinct population in eastern Asia is lacking, and *A. marila* is best considered to consist of only the Eurasian *A. m. marila* and the American *A. m. nearctica.* There is some interchange of the two subspecies in migration. *Received 13 Dec. 1985, accepted 4 Mar. 1986.*

The American Ornithologists' Union (AOU 1957) used the name *Aythya marila nearctica* Stejneger, 1885, for the North American subspecies of the Greater Scaup. More recent authorities use *A. m. mariloides* (Vigors, 1839) for the North American population (Bellrose 1976, Palmer 1976) or for a population in North America and eastern Asia (Johnsgard 1975, 1979). Others (Portenko 1972) recognize both an east Asian *mariloides* and an American *nearctica* in addition to the European *A. m. marila,* and still others (Vaurie 1965) treat *A. marila* as monotypic. Who is correct?

The name *Anas marila* was applied by Linnaeus (1761) to the Scaup Duck of Europe, the species now called in North America the Greater Scaup. In the intervening years the species has been placed in a number of genera, but generic placement will be ignored here. Generic names mentioned beyond, in full or as initials, are all synonymous with the modern *Aythya* and will be used without comment.

It was recognized early that the Scaup Duck of Linnaeus occurred also in the New World (Pennant 1785, Wilson 1814) and across northern Asia (Pallas 1831). It is only in retrospect that we are able to realize that many of the early references to American scaup applied, totally or partly, to another species, now known as the Lesser Scaup, *A. affinis.* Richardson (*in* Swainson and Richardson 1831) seems to have been the first to realize that 2 kinds of scaup occur in North America. Richardson wrote (p. 453): "Our specimens are smaller than English ones killed in the winter, the

[1] This paper is dedicated to John W. Aldrich on the occasion of his 80th birthday.

[2] Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

head, bill, wings, and legs, in particular, being proportionally smaller, and the bill less high at the base . . . but an attentive examination of a number of specimens disclosed no peculiarities which could characterize it as a distinct species, except its size. The undulated markings on the back and wings are darker and less extended than in the English specimens." In what amounts to a parenthetical statement, he also noted that "A *variety,* nearly corresponding with the English one in size, is also found in the fur-countries. . . ." Wing lengths given equate to 196 mm for the smaller birds, and 224 mm for both the larger American variety and the English birds. In describing the bill of the scaup, Richardson (op. cit.) referred to the unguis (nail) as "small and distinct" as in the Pochard, *A. ferina,* and the Canvasback, *A. valisineria.* This description indicates certainly that his basic account is about what later would be known as *A. affinis.*

Eyton (1838) distinguished the present *Aythya affinis* as an American species distinct from *marila,* which he apparently considered strictly an Old World species. Smaller size and the narrower nail on the bill formed the main bases of the separation, as these characters still do. The type, from "North America," is in the British Museum (Natural History) (BMNH) (Salvadori 1895, Warren 1966). One wonders if this is a bird that Richardson had studied; the name certainly applies to the birds he had discussed.

Vigors (1839) was the next to provide a name for a scaup population, although the name was used provisionally and the precise origin of the birds was not stated. In reporting on the birds collected during the voyage of the *Blossom,* under Captain F. W. Beechey, in 1825–1828, Vigors wrote as follows under the heading *Fuligula Marila*: "Several specimens of a bird nearly allied to this species, if not the same, were brought home by the expedition. They uniformly differ from the typical *Ful. Marila* in their smaller size, in the black colour on the breast being less intense and defined, in the undulating white markings being less diffused over the scapulars and back, and being wanting almost entirely on the wing-coverts. Dr. Richardson, whose judgement on these points, and whose experience respecting the birds of the Arctic region entitle him to every confidence, is inclined to consider these birds but as a variety of the European species. Following his opinion, I refrain from describing them as separate. It is however to be observed, that the true *Fuligula Marila* is found in North America, and there is therefore less reason to believe the birds alluded to above to be varieties resulting from climate or locality. Should the species prove to be distinct, the specific name of *Mariloïdes,* which has been suggested by Dr. Richardson, would be appropriate."

Publication of the results of the Beechey expedition had been delayed considerably, and Richardson (and perhaps others) had access to the

specimens well before Vigors's account appeared. Richardson was offered the opportunity to incorporate into his own work a list of species from the northwestern American coast, but declined because (Swainson and Richardson 1831:xiii) "very few of the specimens brought home on that Expedition had notes attached to them to indicate their locality, so that the native places of many are uncertain." It is obvious, however, that the small birds that Vigors had were the same as the smaller scaup that Swainson and Richardson (1831) discussed. Yarrell (1843) discussed two species of scaup, and used the name *mariloides* for the smaller American birds without mentioning the name *affinis*. Yarrell both described and figured a single specimen of what he thought was the smaller American scaup. That bird, which had been bought in a market in England, was later identified as a hybrid *A. ferina* × *A. marila* (Salvadori 1895). Both the description and illustration apply remarkably well to the Redhead, *A. americana*. Interestingly, Audubon (1844) gave Yarrell credit for the first good description of *mariloides*.

Eyton's (1838) name for the small American scaup, *affinis*, was routinely overlooked or ignored by British authors (e.g., MacGillivray 1852). However, Baird (*in* Baird, Cassin, and Lawrence 1858) recognized *affinis* as the name of the smaller species, and treated *mariloides* Vigors as a synonym. Schlegel (1866); Gray (1871); and Baird, Brewer, and Ridgway (1884) treated the two names in the same way. This synonymy would seem to have been firmly established.

Meanwhile, Swinhoe (1873) detected two size classes of scaup in China. The abundant, and apparently regularly occurring, form he recognized as *marila*. Some smaller birds brought to him, from one or two flocks, posed a problem in identification. Swinhoe first considered them to be *affinis*, because of their size and after consultation of works by Yarrell and Baird (presumably those cited above). Those birds, however, had extensive white wing markings that MacGillivray (1852) and Schlegel (1866) attributed to *marila* rather than to *affinis*, and the combination of size and wing characters led Swinhoe to reject either name as applicable. He stated: "Our bird, then, is not the American *F. affinis*; but it nevertheless must be the bird that Mr. Yarrell mentions under the head 'American Scaup,' which was brought home by Capt. Beechey from Behring's Straits, and was apparently identified with that species. Sir John Richardson suggests for this Pacific species the name *mariloides*, which is generally regarded as a synonym of *affinis*. But I think it can now be shown that *F. mariloides* is a species of itself, and a visitant to the Chinese coast. *Fuligula marila* also occurs here in abundance. . . ." This is the first suggestion in the literature that the birds from Beechey's voyage were from the Bering Straits, or that the name *mariloides* referred to a Pacific species. These

concepts may have been derived from the long title of the work in which Vigors (1839) proposed the name *mariloides,* but were counter to the then generally accepted notion that *mariloides* was an American form.

In a report on birds from the Commander Islands, Stejneger (1885) continued to associate *mariloides* with *affinis,* giving the former subspecific rank and assigning to it a range on the "Pacific coast of Asia, from Japan southward," where no scaup was known as a breeding bird. At the same time, Stejneger distinguished the North American population of Greater Scaup from the European birds, under the new name *A. m. nearctica.* Stejneger's account is confusingly written, but it is clear that he considered his specimens from Bering Island (one of the Commander Islands) to be *A. m. marila,* and he presented measurements only for those birds, not for the American form that he named. It seems obvious that he took his concept of the range of *mariloides* from Swinhoe (1873), not recognizing that the latter's discussion referred only to wintering birds.

Seebohm (1890) wrote of *marila* in Japan that "Fully adult males from Japan are precisely similar to those from the British Islands." He pointed out that the amount of white on the wing, used by MacGillivray (1852) and Schlegel (1866) as a specific character and by Stejneger (1885) as a subspecific character, was actually age related. Seebohm treated "*Aythya affinis mariloides* Stejneger" as a synonym of *marila,* which he considered monotypic. Thus Seebohm transferred *mariloides* from the synonymy of *affinis* to the synonymy of *marila.*

Salvadori (1895) presented synonymies for the scaup following Stejneger's (1885) distributional scheme but including both *nearctica* and *mariloides* as part of a monotypic species *marila.* The A.O.U. (1899) followed Salvadori in treating both *marila* and *affinis* as monotypic.

In a discussion of the European *marila,* Dresser (1903) gave specific status to both the American *nearctica* and the East Asiatic *mariloides,* without comment or more detailed delineation of range. Millais (1913) included "Kamtschatka and the Commander Isles" in the breeding range of *marila,* noting that "These Asiatic Scaup frequenting the two last-named places have been separated recently under the name of *F. mariloides* (Vig.)." The association of those breeding grounds with *mariloides* may have resulted from a careless reading of Stejneger's (1885) work, but amounted to a compounding of the errors of several previous authors. Millais cast doubt on the validity of both *mariloides* and *nearctica* as recognizable forms, but for the first time treated *affinis* as a subspecies of *marila.*

Hartert (1920) finalized the association of the name *mariloides* with the Commander Islands-Kamchatka breeding scaup. He noted but rejected Stejneger's arrangement of scaup populations, stating that: "I find

that all specimens from the Far East—i.e. from Japan and China *and* from the Bering Island—are (with few exceptions) smaller than European *N. m. marila,* the wings of 16 adult male examples measure 207–220 mm., in the European form 220–230 mm. Moreover, in nearly all cases the black barring of the upperside is coarser, thus giving the latter a darker appearance, which is particularly noticeable on the scapulars. . . . We must therefore, unless we suppress this form altogether, recognize a Far-East form breeding on Bering Island, and probably in Kamtchatka, wintering in China and Japan." Hartert recognized three subspecies of *marila*—*nearctica* in North America; *marila* in Europe and northern Asia, with indefinite Asian limits; and *mariloides* breeding on Bering Island, probably Kamchatka and elsewhere, wintering in eastern Asia. He noted that the latter population is closely allied to *marila,* not to *affinis.* Hartert's separation of *marila* from *mariloides* at a wing length of 220 mm is directly opposed to Seebohm's (1890) and Salvadori's (1895) analyses.

Peters (1931) followed Hartert's classification of the scaup, and additionally fixed the type locality of *mariloides* by giving it as "No type locality = Bering Sea." No reason for this decision was given and one might guess that Peters, as perhaps Swinhoe (1873) earlier, was influenced by the title of the work in which *mariloides* was named and also by Hartert's use of the name for the Bering Island population. Hartert's classification was also accepted by Hellmayr and Conover (1948). Dement'ev and Gladkov (1952), however, did not recognize any subspecies of *marila,* noting that the amount of variability in the supposedly differentiating characters was great. The A.O.U. (1957) again accepted the name *nearctica* for the North American population of Greater Scaup, following Peters (1931) and Hellmayr and Conover (1948).

Parkes (1958), noting that several authors had doubted the valid distinction of *nearctica,* examined the series of specimens in the American Museum of Natural History (AMNH) "and found that *nearctica* is readily recognizable by the coarse black barring of the upper parts, exactly as characterized by Hellmayr and Conover. . . ." He considered *mariloides* "of eastern Asia" to be intermediate in color but smaller than either *marila* or *nearctica,* citing Hartert's measurements.

Delacour (1959) recognized two subspecies of *A. marila,* the nominate form in Europe and western Asia and *mariloides* in eastern Asia and North America, merging *nearctica* into the latter. His measurements of wing length give *mariloides* a greater range of variation than *marila,* and one that completely encompasses the latter. Palmer (1976) followed Hellmayr and Conover (1948) and Parkes (1958) in separating American from Eurasian birds on the basis of back color, but recognized only two subspecies. To the American population, however, he applied the name *mar-*

*iloides,* treating *nearctica* as a synonym. Thus he followed Delacour in the use of the name for the American population but not in the range allotted to it, dropping the Asian population whose birds were supposedly the basis of the name. Bellrose (1976) used the same names in the same fashion. Johnsgard (1975, 1979) followed the taxonomic arrangement of Delacour.

## DISCUSSION

Two problems are revealed by the preceding taxonomic history. The first involves the allotment of the name *F. mariloides* Vigors, 1839 to either *marila* or *affinis.* The second is whether there is a recognizable population of scaup in the Commander Islands and Kamchatka.

It is quite clear that the small birds with the narrow unguis that Richardson discussed in 1831 and that Vigors named *mariloides* in 1839 were the same, and that Eyton named that form *affinis* in 1838, while Vigors's manuscript on the voyage of the *Blossom* was awaiting publication. Both European and American authors accepted *mariloides* as the smaller of the American species of scaup, often treating it as a synonym of *affinis,* into the 1870s and beyond. It was not until Swinhoe (1873), confused by Yarrell's (1843) description of a hybrid as *mariloides* and other misinformation, associated that name with birds "from Behring's Straits" that the concept of *mariloides* as an Asian population originated. This concept was repeated by Stejneger (1885), who nonetheless maintained the association of *mariloides* with *affinis.* Once *mariloides* was accepted as referring to an Asian population, it was logical to consider that the name was synonymous with *marila,* because *affinis* does not occur in Asia. Thus Seebohm (1890) and Salvadori (1895), even as they denied the validity of the taxon *mariloides,* associated the name with European *marila.* By 1920, the "fact" that the name *mariloides* applied to east Siberian birds, specifically those of the Commander Islands and nearby Kamchatka, was accepted, the only question then relating to the distinctness of the population. That "fact" was finally given some basis when Peters (1931) formally designated "Bering Sea" as the type locality of *mariloides.*

Although no locality was given for the scaup specimens that Vigors discussed, and no type was (or has been subsequently) designated, the specimens almost certainly originated in North America. Vigors (1839) wrote about 102 species of birds in his report on Capt. Beechey's voyage; 68 of these are American species, whereas only 3 are strictly Palearctic. Of the other ducks discussed, 5 are strictly American and 4 are Holarctic in distribution. The form of *Anas crecca* discussed was *carolinensis,* and the only wigeon mentioned was *Anas americana.* At least one duck, the Bufflehead, *Bucephala albeola,* "was found at San Francisco" and several

of the shorebird specimens also were taken there. Probably most of the waterbirds, including the scaup, were taken from large wintering flocks in the San Francisco Bay area or in Monterey Bay, California, as the *Blossom* spent parts of 2 winters in that vicinity (Rosewater 1968). I suggest San Francisco Bay, California, as the corrected type locality for *Fuligula mariloides* Vigors, 1839, *contra* Peters (1931).

The second problem is whether the east Asian and North American populations of *marila* are distinct from the European population and, if so, what the limits of their ranges are. The present consensus is that North American birds differ from European birds by having coarser and more extensive black vermiculation on the mantle (Hartert 1920, Hellmayr and Conover 1948, Parkes 1958, Delacour 1959, Portenko 1972, Palmer 1976), yielding a darker back overall. This character is restricted to adult males, a fact not always stated; no one has ever suggested that other sex or age classes could be distinguished. My examination of specimens supports this consensus, and the validity of *nearctica,* although the character does not provide 100% separation. A small proportion of American birds are nearly as white on the mantle as European birds, as noted by Bishop (1895).

The supposed characteristics of the eastern Asian population have been confusingly set forth by various authors, partly because of the confusion over the specific application of the name *mariloides* and partly because that population was compared to different populations at different times. Smaller size and darker dorsal color relative to European *marila* have been invoked as distinguishing features, as has paler color relative to American birds.

Swinhoe (1873) first reported small scaup from Asia, but gave no measurements or any basis for his characterization of the birds. Both Seebohm (1890) and Salvadori (1895) denied that Asian birds (including those sent to England by Swinhoe) were consistently smaller than European ones. Hartert (1920) repeated that Asian birds were smaller "with few exceptions," and provided ranges of measurements to support his statement. His figures divided European and Asian birds at a wing length (adult male) of 220 mm, not allowing for any of the "exceptions." Portenko (1972) suggested an average size difference and stated that "specimens with much shorter wings predominate" among Asian birds relative to those of Europe, although the ranges of measurements given virtually overlap. No other authors have given measurements specifically for the Asian population, except Stejneger (1885) for 2 males.

Available measurements from many sources (Fig. 1) do not indicate that Asian birds have shorter wings. Hartert's Far East sample is at the lower end of the range of variation, but overlaps most samples of European

birds and, as noted above, apparently omits any exceptional birds. Portenko's East Asian sample is small in wing length but so is his West Asian sample compared to others, and the means of his two samples differ only slightly. The mixed samples that include Asian birds, those of Delacour, Palmer, and Dement'ev and Gladkov, do not, except for the last, show any great tendency to include small birds. My own measurements of the chord of several samples (Table 1) (Fig. 1) show primarily that most other writers must have measured the flattened wing, and secondarily that there is no great amount of geographic variation. I conclude that there is no evidence indicating that eastern Asian *marila* are recognizably smaller than European or North American ones.

As indicated above, adult males of the European and North American populations can be distinguished by back color. Hartert (1920) considered East Asian birds to be darker than European ones, with those of America the same or even darker. Parkes (1958) and Portenko (1972) considered them to be intermediate. Delacour believed Asian birds to be the same as American ones, a view endorsed by Alexander Wetmore on examination of specimens in the British Museum (Natural History) (in litt. to L. L. Short, FWS files).

I compared 10 adult males from Siberia, Japan, and Bering Island in the AMNH and U.S. National Museum of Natural History (USNM) with larger series of European and North American birds. As a series the Asian birds seem to me to be more similar in dorsal appearance to European specimens than to American birds, although one winter bird from Japan and 2 worn breeding birds from Bering Island might be classed as intermediate. I also examined several first-year males from Asia and noted that they tend to be darker than the adults, approaching the American birds. It is possible that age classes were not adequately separated in some previous comparisons. I conclude that Asian birds cannot be distinguished from European ones on the basis of dorsal color any more than they can on size. I recommend, therefore, that only two subspecies of Greater Scaup be recognized, *A. m. marila* of Eurasia and *A. m. nearctica* of North America.

## DISTRIBUTIONAL RECORDS

The Pribilof Islands represent a landfall for many migrant birds from both North America and Asia, and have provided the first and only American records of several Old World species or subspecies. I have examined 5 adult males of *Aythya marila* from the Pribilof Islands in the USNM and the University of Kansas Museum of Natural History. One specimen taken in late April and 3 in early June are dark dorsally like typical North American birds. One specimen, USNM 496822, taken 29

FIG. 1. Measurements of wing length of male (presumably adult, but not stated in every instance) Greater Scaup. Sources: 1, Palmer (1976); 2, Oberholser (1974); 3, Delacour (1959); 4, Stejneger (1885); 5, Hartert (1920); 6, Portenko (1972); 7, Cramp and Simmons (1977); 8, Bauer and Glutz von Blotzheim (1969); 9, Witherby et al. (1939); 10, Dement'ev and Gladkov (1952); 11, this study, Table 1. A dash under N indicates an unspecified sample size.

TABLE 1
WING CHORD (MM) OF ADULT MALES OF POPULATIONS OF GREATER SCAUP, MEASURED BY THE AUTHOR

| Area | N | Range | Mean |
|---|---|---|---|
| North America | 25 | 205.5–222.5 | 215.7 |
| Europe | 12 | 206.5–218.0 | 214.6 |
| Eastern Asia | 10 | 205.0–223.5 | 210.9 |
| Pribilof Islands | 4 | 211.0–217.0 | 214.6 |
| All areas | 51 | 205.5–223.5 | 213.9 |

June 1968 on St. George Island by Max C. Thompson, is much paler on the back and is identical in that feature to birds from Europe and Japan. I consider this bird a representative of the Eurasian population, *A. m. marila.* Despite the date, this bird had small testes, and the species apparently does not breed on the Pribilofs. This appears to be the only record of the Eurasian subspecies in North America. The pale color of this individual, incidentally, supports the rejection of the concept of a darker east Asian subspecies; it is unlikely that a European bird would have reached the Pribilofs.

Greater Scaup from North America occasionally migrate, or wander, to Asia. One such bird was banded on 17 September 1977 on Amchitka Island in the Aleutians and recovered on 21 October 1977 on the island of Hokkaido, Japan. This bird was a female that was banded in the year it hatched and probably was a locally hatched bird although it was capable of flight and may have reached Amchitka from another area (C. F. Zeillemaker, pers. comm.). This is the only record of *A. m. nearctica* in Japan or elsewhere in Asia.

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# FOOD CONSUMPTION AND GROWTH ENERGETICS OF NESTLING GOLDEN EAGLES

MICHAEL W. COLLOPY[1]

ABSTRACT.—Food consumption, energy metabolism, and growth of 12 wild Golden Eagle (*Aquila chrysaetos*) chicks were compared with 4 captive chicks to evaluate the influence of food availability and sibling interaction on growth in wild nestlings. Captive female and male eaglets consumed and assimilated similar amounts of black-tailed jack rabbit (*Lepus californicus*). A linear relationship between age and maximum meal size was used in conjunction with field estimates of crop fullness to refine calculations of daily consumption. Growth of captive chicks was very similar to patterns exhibited by wild nestlings. Among wild nestlings, however, females had significantly heavier asymptotic body weights, but slower growth rates than males. Growth curve inflection points occurred 2.2 days later for females than for males, but the difference was not significant. The energy metabolized (ME) by captive and wild female eaglets showed similar increasing trends throughout the chick-rearing period. ME values for captive and wild males, however, differed substantially. Wild male eaglets had reduced ME values during the sixth week of chick rearing, a time when captive males showed peak consumption rates. This difference may have been due to the presence of sibling competition, principally with females, for food. *Received 20 May 1985, accepted 7 Mar. 1986.*

Previous work on nesting Golden Eagles (*Aquila chrysaetos*) has focused mainly on diet and nesting biology (see MacPherson 1909, Gordon 1927, Bent 1937, Carnie 1954, Mollhagen et al. 1972, Smith and Murphy 1973). A few studies quantified food requirements using captive (Fevold and Craighead 1958) and wild (Brown and Watson 1964, McGahan 1967) eagles. Several of these nesting studies also reported growth patterns of eaglets, but none concurrently quantified the food consumption of young.

Here I document the food consumption, energy metabolism, and growth rates of captive Golden Eagle nestlings, and compare these values with consumption and growth rates of nestlings in the wild. I also discuss differences between wild and captive chicks in relation to the effects of sibling competition and food availability on the growth of wild eagles.

## STUDY AREA AND METHODS

*Field study.*—The study area was within the Snake River Birds of Prey Area (BPA) and included the Snake River Canyon and surrounding upland desert plateau south of Boise, Idaho, in Owyhee and Elmore counties. The BPA, administered by the Bureau of Land Management, lies within the Great Basin semidesert scrub biome described by Whittaker (1975). Major vegetation types in the area include big sagebrush (*Artemisia tridentata*)

[1] School of Natural Resources, Univ. Michigan, Ann Arbor, Michigan 48104. (Present address: Dept. Wildlife and Range Sciences, 118 Newins-Ziegler Hall, Univ. Florida, Gainesville, Florida 32611.)

associations, shadscale (*Atriplex confertifolia*), and grasses (*Poa* and *Bromus* spp.) (U.S.D.I. 1979).

I observed the offspring of 4 pairs of Golden Eagles in or near the BPA throughout the nesting season in both 1978 and 1979. Because each breeding pair fledged young in 1978, and subsequently nested in the same nests in 1979, I assumed that my presence did not seriously disturb the birds. I monitored the feeding behavior of nestlings from blinds placed 15–40 m away from the nest during 24-h observation periods (noon to noon). At the end of each meal, I estimated the percent fullness of each chick's crop (0, 25, 50, 75, or 100% full). The amount of food consumed by each nestling was calculated using the estimate of crop fullness and the linear relationship describing maximum meal size as a function of age, established with captive male and female chicks (see Results). Estimates of the mean amount of energy metabolized daily (ME) were obtained for male and female nestlings during each week of chick rearing by multiplying the mean daily consumption rates by the efficiency with which black-tailed jack rabbits (*Lepus californicus*) were digested and assimilated (established using captive young). Wild nestlings consumed other vertebrates in addition to jack rabbits, and I assumed their ability to digest and assimilate these prey was similar to that for rabbits.

After each observation period, I climbed to the nest and weighed each nestling, measured its foot-pad length (Kochert 1972), and estimated the percent fullness of its crop and calculated the corresponding biomass in the crop. The corrected body weight of each chick was calculated by subtracting the estimated biomass of food contained in the crop from the total body weight (Collopy 1983). Sex of the study birds was assigned using a discriminant function derived from body weight and foot pad measurements on eagles of known sex (Edwards and Kochert, in press). Measurements of hallux claw length and culmen length (see Bortolotti 1984a) were not taken, so discrimination based on these characters was not possible.

Weight data were analyzed using the Statistical Analysis System's (SAS) nonlinear least squares curve-fitting procedure (NLIN). Logistic and Gompertz growth models were used to fit curves to both male and female weights (Ricklefs 1968). The logistic model best fit the data (Ricklefs, pers. comm.), and I used it to calculate the growth rate constants ($K$), asymptotic body weights ($A$), and inflection points ($t$) of both captive and wild eaglets.

*Captive bird study.*—In 1978 and in 1979, two Golden Eagle chicks, 10–14 days old, were taken from nests in or near the BPA for use in feeding trials. At the conclusion of the experiments the nestlings were placed in foster nests in the wild from which they fledged successfully. Sex of the nestlings again was assigned based on body weight and foot-pad measurements taken just prior to release; we studied 2 females in 1978 and 2 males in 1979.

The study birds were housed in an unheated, enclosed building 4.0 m long, 1.8 m wide, and 2.5 m high. Each eaglet was isolated in an uncovered wooden cubicle inside the structure. Initially, dimensions were 0.7 m × 0.9 m. Later, as the birds grew and required more space, cubicle size was enlarged to 1.0 m × 1.9 m.

Black-tailed jack rabbits, the predominant prey species of Golden Eagles in southwestern Idaho (U.S.D.I. 1979), were used as food in the feeding trials. As the energy content of small mammals can exhibit considerable seasonal variation (Gorecki 1965, Schreiber and Johnson 1975), and as I was attempting to feed the captive chicks a diet normally encountered in the wild, I used jack rabbits that were collected periodically during the feeding experiments. Jack rabbits were collected on 12 April, 7–12 May, and 17 May in 1978, and on 11 April, 25 April, 9 May, and 15 May in 1979. Each whole jack rabbit was weighed, the stomach and intestines removed, and the carcass homogenized using a meat grinder. To guard against possible vitamin and mineral deficiencies, calcium and multiple vitamin supplements were supplied daily to each chick.

Seven consecutive feeding trials were conducted with each captive chick. The duration of each trial ranged from 5 to 7 days. Every morning before the first meal, the birds were weighed on spring scales, and any regurgitated pellets were collected. During each feeding experiment, the study birds were fed approximately the same number of meals daily that I observed wild nestlings of the same age receive (Collopy 1980); however, captive birds were allowed to feed until satiated. The biomass of food consumed at each meal was calculated by subtracting the amount remaining at the end of the meal from the total weight of food presented to the bird. All excrement voided during the course of each experiment was collected from plastic sheeting used to line the cubicles.

The total weights of pellets and excrement obtained during each feeding experiment were determined after oven drying to a constant weight at 65°C. Percent water contained in jack rabbits from each collection was calculated by drying the samples at 65°C and determining the percent weight loss. Fat was extracted from the samples of eagle pellets and excrement with petroleum ether (Soxhlet method; Horwitz 1975), and from samples of all collections of black-tailed jack rabbits. Percent fat in all samples of jack rabbits, eagle pellets, and excrement was determined indirectly by calculating the percentage of material lost following the fat extraction. Energy content (kJ/g) of samples of fat extracted from food, and fat-free extracts from food, pellets, and excrement associated with each feeding trial were analyzed in a Parr adiabatic bomb calorimeter.

Energy ingested (I), egested (E), and metabolized (ME) by each chick during each experiment was calculated from the biomass consumed and the caloric contents of black-tailed jack rabbits, eagle pellets, and excrement. I, E, and ME are expressed in kJ/day. The efficiency with which food was digested and assimilated (i.e., assimilation efficiency, AE = ME/I) by each study bird was calculated for each feeding experiment. Percentage data were arcsine transformed prior to statistical analysis to meet the assumptions of the statistical models. All means are presented with standard errors (± SE).

## RESULTS

*Composition and energy content of black-tailed jack rabbits.*—A total of 92 black-tailed jack rabbits were collected in the BPA during 1978 and 1979. Between-year comparisons of mean body weights showed that both males ($t = 2.2$, $P = 0.03$) and females ($t = 3.8$, $P = 0.0005$) were significantly heavier in 1979 than in 1978. Energy content of jack rabbits, expressed on a live-weight basis, was 5.54 ± 0.09 kJ/g (N = 3) in 1978 and 6.51 ± 0.17 kJ/g (N = 4) in 1979 ($t = 4.6$, $P = 0.006$). This difference resulted from the greater percentage fat content in jack rabbits collected in 1979 (9.0 ± 0.88%) than in 1978 (3.3 ± 0.42%). The energy content (dry weight) of jack rabbit fat was 39.18 kJ/g (N = 1) in 1978 and 43.71 ± 1.93 kJ/g (N = 4) in 1979.

*Food consumption.*—Substantial variation was observed in the amount of food consumed each day by the captive nestlings. Patterns in food consumption were apparent, however, when the amount of food consumed daily by females and males was summarized for each feeding trial (Table 1). For each individual, mean daily food consumption increased steadily during the first three trials, peaked during trials 4 and 5 (28–44 days old), and decreased during the last two trials. A two-way ANOVA

TABLE 1

BIOMASS OF FOOD CONSUMED AND EGESTED BY CAPTIVE MALE AND FEMALE NESTLINGS DURING EACH FEEDING TRIAL IN 1978 AND 1979

| Year | Individual | Feeding trial | Initial | | Mean daily biomass consumed | | Mean daily biomass egested | |
|---|---|---|---|---|---|---|---|---|
| | | | Age (days) | Weight (g) | Wet weight (g/day) | Dry weight (g/day) | Pellets (g/day dry weight) | Excrement (g/day dry weight) |
| 1978 | Female 1 | 1 | 15 | 1012 | 442 | 135 | 8 | 47 |
| | | 2 | 21 | 1725 | 541 | 165 | 7 | 59 |
| | | 3 | 26 | 2375 | 572 | 174 | 7 | 69 |
| | | 4 | 32 | 3225 | 610 | 177 | 9 | 75 |
| | | 5 | 38 | 3700 | 522 | 152 | 9 | 68 |
| | | 6 | 45 | 3800 | 480 | 139 | 5 | 65 |
| | | 7 | 51 | 4000[a] | 561 | 162 | 10 | 71 |
| | Female 2 | 1 | 11 | 322 | 240 | 73 | 4 | 29 |
| | | 2 | 17 | 800 | 364 | 111 | 3 | 41 |
| | | 3 | 22 | 1270 | 385 | 117 | 5 | 46 |
| | | 4 | 28 | 1785 | 423 | 123 | 7 | 52 |
| | | 5 | 34 | 2175 | 542 | 158 | 7 | 67 |
| | | 6 | 41 | 2950 | 479 | 138 | 6 | 65 |
| | | 7 | 47 | 3150[b] | 540 | 156 | 8 | 74 |
| 1979 | Male 1 | 1 | 14 | 580 | 249 | 77 | 3 | 33 |
| | | 2 | 20 | 920 | 370 | 114 | 5 | 49 |
| | | 3 | 26 | 1525 | 457 | 141 | 10 | 59 |
| | | 4 | 32 | 2050 | 556 | 180 | 10 | 78 |
| | | 5 | 38 | 2750 | 531 | 168 | 9 | 74 |
| | | 6 | 45 | 3100 | 579 | 195 | 10 | 79 |
| | | 7 | 51 | 3300[c] | 375 | 126 | 11 | 50 |
| | Male 2 | 1 | 11 | 395 | 184 | 57 | 7 | 27 |
| | | 2 | 17 | 670 | 312 | 96 | 4 | 43 |
| | | 3 | 23 | 1225 | 408 | 126 | 7 | 50 |
| | | 4 | 29 | 1890 | 495 | 160 | 8 | 68 |
| | | 5 | 35 | 2550 | 508 | 161 | 7 | 68 |
| | | 6 | 42 | 3000 | 456 | 153 | 11 | 63 |
| | | 7 | 48 | 3050[d] | 351 | 118 | 6 | 51 |

[a] Final weight = 4150 g.
[b] Final weight = 3500 g.
[c] Final weight = 3250 g.
[d] Final weight = 3100 g.

comparing captive male and female Golden Eagle chicks showed no significant difference between their mean daily consumption rates during the feeding experiments ($F = 4.08$, $P > 0.20$).

Food consumption during one meal each day tended to be much greater than all others. I assumed that this particular meal was at or close to the

TABLE 2

MEAN NUMBER OF MEALS PER DAY AND MEAN DAILY FOOD CONSUMPTION BY WILD FEMALE AND MALE GOLDEN EAGLE NESTLINGS DURING EACH WEEK OF CHICK REARING IN 1978 AND 1979

| Week of chick rearing | Mean number of meals per day | | Mean daily food consumption | | | |
|---|---|---|---|---|---|---|
| | | | Female (N = 6) | | Male (N = 6) | |
| | No./day | SE | g/day | SE | g/day | SE |
| 1 | 4.1 | 0.7 | 54 | 41 | 40 | 3 |
| 2 | 3.0 | 0.8 | 62 | 21 | 139 | 24 |
| 3 | 3.4 | 0.8 | 160 | 61 | 277 | 39 |
| 4 | 2.6 | 0.5 | 247 | 56 | 349 | 55 |
| 5 | 2.6 | 0.7 | 247 | 112 | 336 | 40 |
| 6 | 3.3 | 0.8 | 333 | 97 | 276 | 34 |
| 7 | 3.9 | 0.5 | 415 | 54 | 376 | 50 |
| 8 | 4.3 | 0.6 | 691 | 140 | 381 | 45 |
| 9 | 4.0 | 0.9 | 579 | 163 | 366 | 136 |
| 10 | 2.4 | 0.7 | 310 | 119 | 245 | 43 |

maximum possible for a bird at that stage of development. These maximum meal-size data were subjected to logarithmic transformation prior to analysis, as their variance increased with the age of the chicks. Simple linear regression analyses demonstrated that maximum meal size ($Y$) and age ($X$) were significantly related for both captive male and female chicks (males: $\log Y = 1.747 + 0.017X$, $r^2 = 0.82$; females: $\log Y = 1.710 + 0.021X$, $r^2 = 0.83$), and that the slopes of equations derived for female young were significantly steeper ($P < 0.001$) than for males. This indicated that as sexual dimorphism in size increased with age (see also Bortolotti 1984b), females were capable of consuming more food per meal than were males.

I estimated the mean daily food consumption of wild nestlings (Table 2) using the maximum meal size vs age relationship established with captive chicks, the crop fullness following each meal, and the number of meals. Daily food consumption by male and female eaglets varied greatly depending on the number and size of prey delivered by parents. Although females consumed more food than males late in chick rearing, the sexes were not significantly different in the mean amount consumed daily during each week of chick rearing ($F = 0.49$, $P > 0.20$). Furthermore, during the last half of the chick-rearing period, daily food consumption of both wild and captive eaglets was consistently greater than estimates of adult food consumption (Brown and Watson 1964, McGahan 1967).

*Growth.*—Increases in body weight of male and female Golden Eagle

chicks (Fig. 1) conformed with the growth curves of other captive and wild eaglets (Sumner 1929, 1933; Kochert 1972; Ellis 1979). Although only two male and two female chicks were tested, a comparison of the parameters that describe logistic curves fit to the growth data showed that captive female chicks had asymptotic body weights ($A$) 518 g heavier than males, while the growth rate constants ($K$) and inflection points ($t$) of both sexes were similar (Table 3). Weight gains of captive female chicks showed greater individual variation than those of males (Fig. 2) because one female chick was in relatively poor condition when first acquired.

Growth parameters also were calculated for the wild male and female nestlings (Table 3). Female chicks had asymptotic body weights ($A$) 636 g heavier than males ($t = -4.73$, $P < 0.001$). Males had significantly faster growth rates ($K$) ($t = 2.77$, $P < 0.02$). The mean inflection point ($t$) in the growth curves of males occurred 2.2 days sooner than it did for females, but the difference was not statistically significant ($t = -2.01$, $0.05 < P < 0.10$). A statistical comparison between wild nestlings from single chick broods and captively reared individuals was not possible because of small sample sizes; however, growth rates ($K$) of these wild male and female eaglets averaged 0.118 (N = 1) and 0.112 (N = 3), respectively, slightly lower than captive birds of the same sex.

Efficiency of body growth can be expressed as the ratio of biomass production to food consumption (Odum 1959). Captive male and female eaglets both had growth efficiencies that decreased linearly with age (Collopy 1980); however, no significant differences were detected between the regression equations derived for males and females ($F = 0.04$, $P = 0.84$). This inverse relationship reflected the changing pattern of energy allocation to growth during the nestling period. At two weeks of age (feeding trial 1), eaglets converted an average of 27% of the biomass consumed to body weight (Table 1). As the birds approached asymptotic weights, greater proportions of their daily energy budget were allocated to maintenance. This steadily reduced their growth efficiencies to levels below 5% as the birds approached fledging weight.

*Metabolism calculations.*—Percent fat and energy content of fat-extracted (lean) pellets and excrement were calculated for each feeding trial (Table 4). Energy content of fat was taken from direct measurements of jack rabbit fat. Significantly more fat was found in both the pellets ($t = -5.2$, $P < 0.0001$) and excrement ($t = -8.0$, $P < 0.0001$) of captive eaglets in 1979 (males), than in 1978 (females). Simple linear regression analyses demonstrated that the biomass of fat found in both pellets and excrement was dependent largely on the biomass of fat consumed (Fig. 2). This relationship was not apparent when only the 1978 data were considered, as relatively lean jack rabbits limited variation in the amount

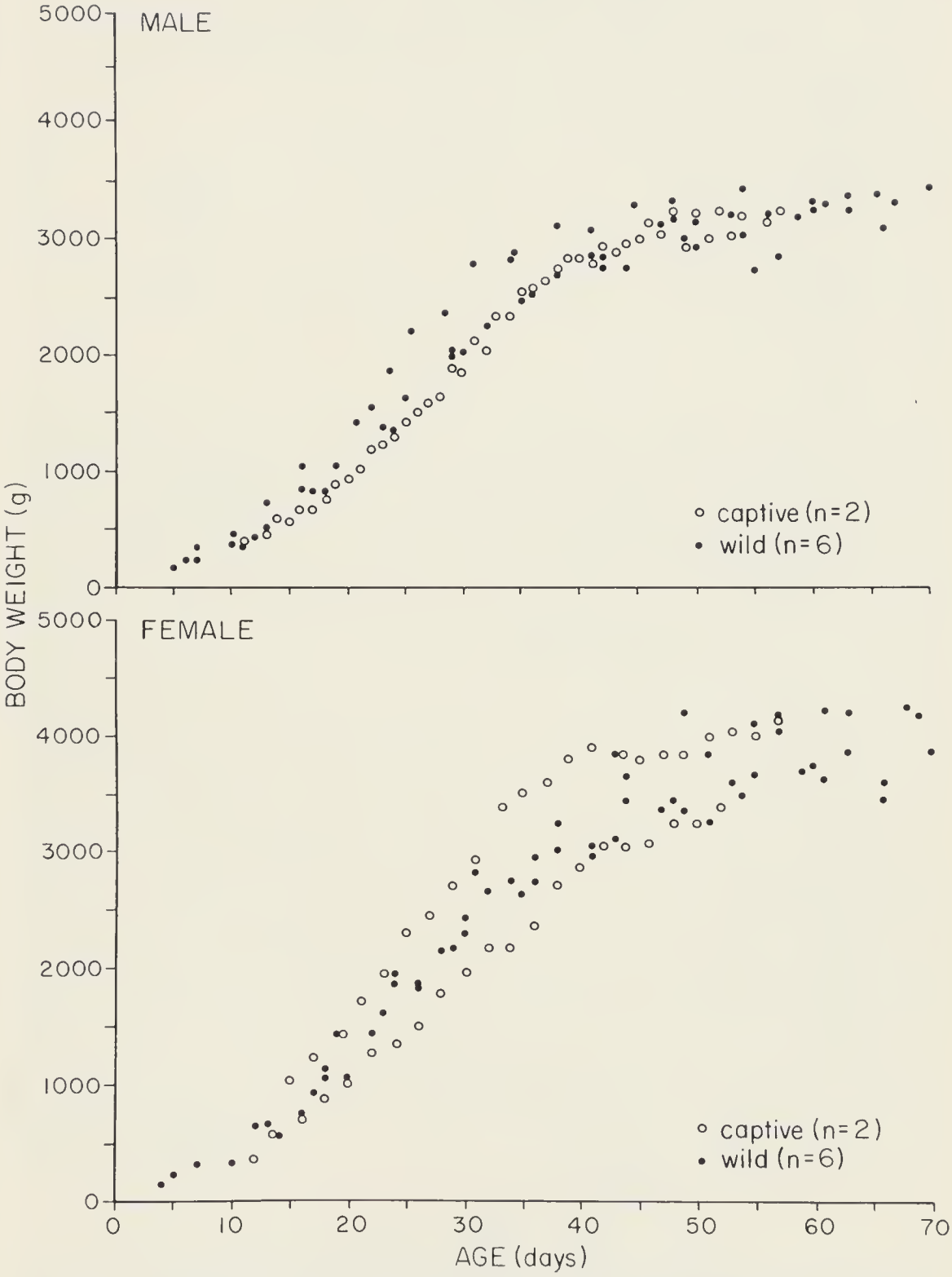


FIG. 1. Body weights of male and female Golden Eagle chicks in relation to age.

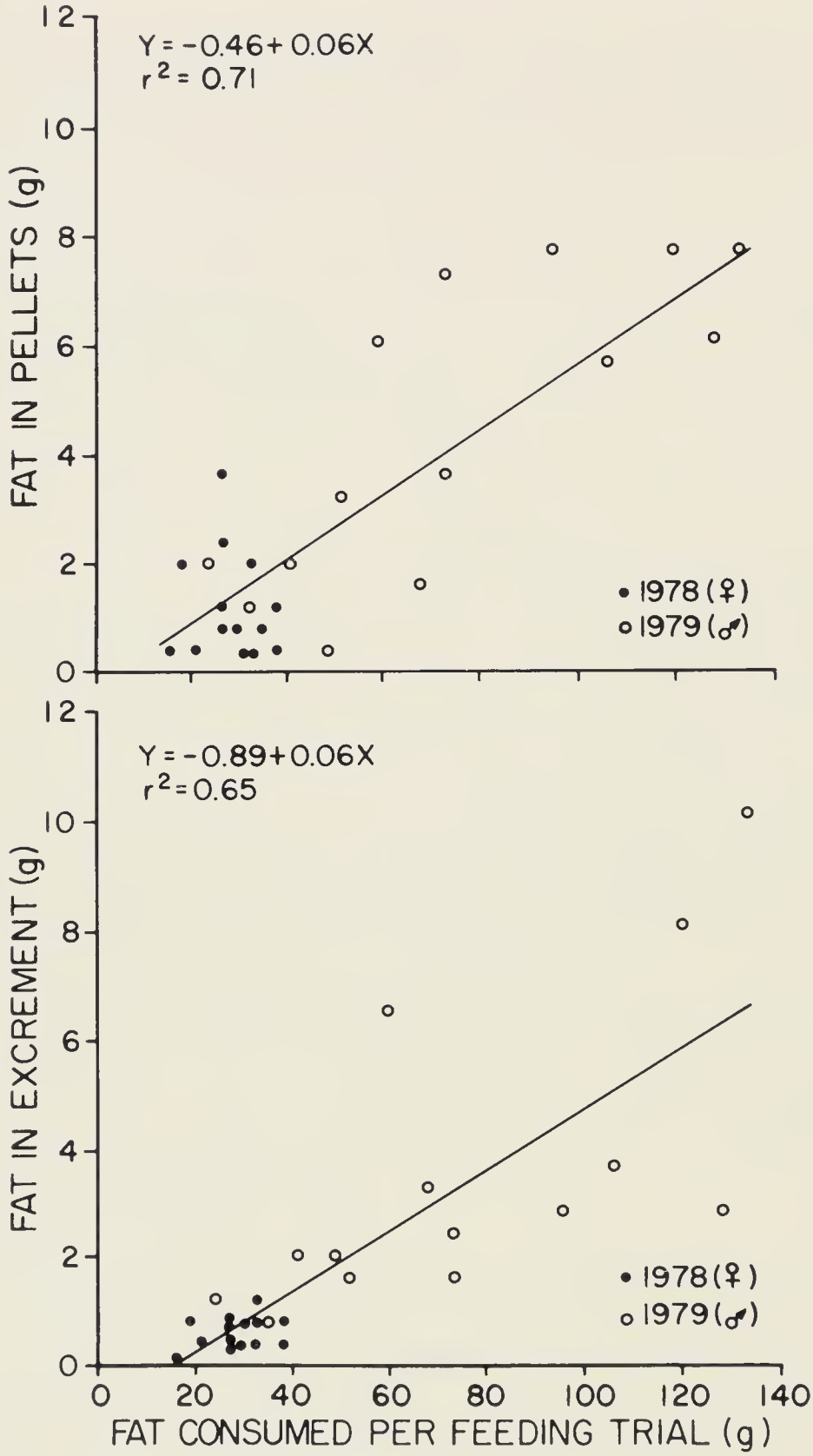


FIG. 2. Cumulative biomass of fat extracted from captive eaglet pellets and excrement collected during each feeding experiment in relation to total biomass of jack rabbit fat consumed.

TABLE 3

LOGISTIC GROWTH PARAMETERS OF FEMALE AND MALE GOLDEN EAGLES MONITORED IN CAPTIVITY AND IN THE WILD DURING 1978 AND 1979

| | | Asymptotic weight (g) | | | Growth rate constant ($day^{-1}$) | | Inflection point (days) | |
|---|---|---|---|---|---|---|---|---|
| Status | Sex | N | *A* | SE | *K* | SE | *t* | SE |
| Wild | Female | 6 | 3834 | 128 | 0.119 | 0.003 | 26.1 | 0.5 |
| | Male | 6 | 3198 | 42 | 0.139 | 0.007 | 23.9 | 1.0 |
| Captive | Female | 2 | 3779 | 235 | 0.127 | 0.016 | 26.0 | 0.8 |
| | Male | 2 | 3261 | 116 | 0.138 | 0.009 | 26.7 | 2.7 |

of fat that the nestlings consumed. In 1979 jack rabbits contained more fat and provided the chicks with an apparent fat surplus in the diet.

Peaks in the amount of energy metabolized daily by captive male and female eaglets occurred at about 2500 kJ/day for both sexes (Fig. 3). Trends in ME for both sexes closely paralleled those of food consumption and were not significantly different ($F = 1.11$, $P > 0.20$). This was due to the relatively constant assimilation efficiencies among the 4 captive birds ($\bar{x} = 74.4\%$, range = 73.9–74.8%). No significant differences in assimilation efficiencies occurred within or between the sexes ($P > 0.50$).

The amount of energy metabolized daily (ME) by wild male and female eagle nestlings during each week of chick rearing was calculated using observed food consumption rates, jack rabbit body composition and energy values, and assimilation efficiencies established using the captive birds (Fig. 3). Although there were no statistically significant differences in ME throughout chick rearing in wild male and female chicks ($F = 0.24$, $P > 0.20$), some differences in the patterns of consumption and metabolism were apparent. Males reached a peak ME value near 1600 kJ/day during weeks 4 and 5, followed by a one-week depression in consumption. ME values once again peaked during weeks 7 and 8 of chick rearing at about 2000 kJ/day. Females showed a consistently increasing trend in ME values, with a peak rate of approximately 3100 kJ/day during week 8 of chick rearing.

## DISCUSSION

Studies of captive nestlings frequently are used to estimate the energy requirements of wild birds. To justify the extrapolation of laboratory data to the wild, food consumption and growth patterns of captive and free-living birds must be similar and measured under comparable conditions.

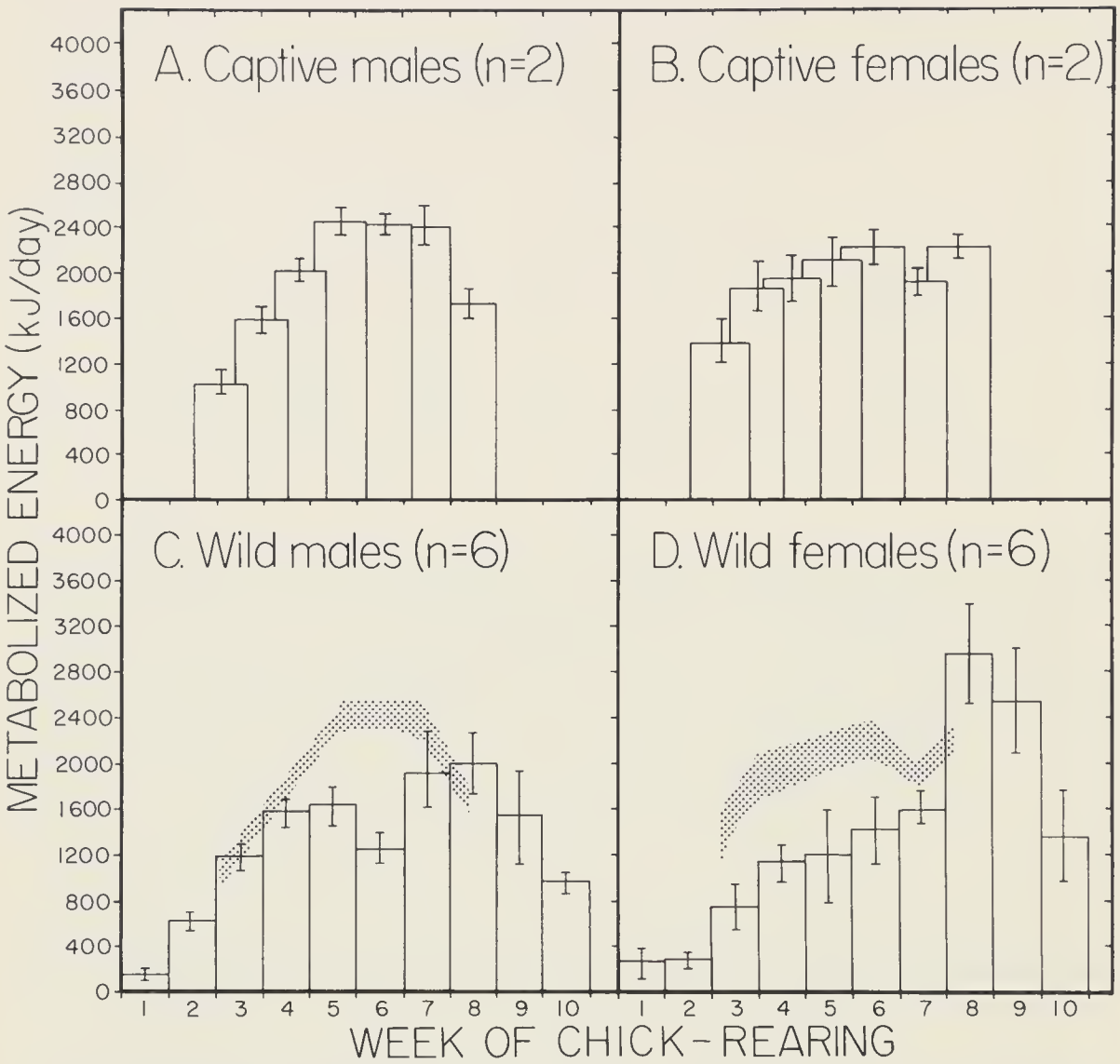


Fig. 3. Mean (± SE) daily metabolized energy of captive male (A) and female (B), and wild male (C) and female (D) eaglets in relation to week of chick rearing. Shaded areas on panels (C) and (D) represent ± SE of the mean for captive male and female eaglets the same age. Overlapping histograms for captive males and females were the result of different-aged eaglets being used in sequential feeding trials.

Some studies have compared the developmental processes of captive and wild nestlings and found no major differences (Junior 1972, Shanholzer 1972, Siegfried 1972). In a study using captive American Kestrels (*Falco sparverius*), however, Bird and Clark (1983) reported that chicks raised by captive parents grew more rapidly and achieved greater size than did hand-reared nestlings. They concluded that lower feeding rates of the hand-reared kestrels limited growth rates.

In this study, Golden Eagle chicks reared in captivity and those monitored in the wild showed little difference in patterns of growth (Fig. 1).

TABLE 4

PERCENTAGE FAT COMPOSITION AND ENERGY (LEAN) CONTENT OF PELLETS AND EXCREMENT PRODUCED BY CAPTIVE FEMALE AND MALE GOLDEN EAGLE CHICKS

| | | | Percentage composition (% dry weight) | | Energy content (kJ/g dry weight) | | |
|---|---|---|---|---|---|---|---|
| | Sex | N | Fat | SE | N | Lean | SE |
| Pellets | Female | 14 | 2.7 | 0.48 | 14 | 16.79 | 0.42 |
| | Male | 14 | 8.7 | 1.04 | 14 | 17.62 | 0.29 |
| Excrement | Female | 14 | 0.15 | 0.01 | 14 | 9.54 | 0.13 |
| | Male | 14 | 0.93 | 0.14 | 14 | 9.25 | 0.17 |

There were, however, some differences between the mean daily metabolized energy values of captive male and female chicks and their wild counterparts. Wild female nestlings consistently assimilated slightly less food than captive females during much of the chick-rearing period (Fig. 3). This difference was not surprising as the captive chicks were provided food *ad libitum,* no doubt in excess of the food available to wild nestlings. In contrast, wild male eaglets had reduced ME values midway through chick rearing when captive males showed peak consumption rates (Fig. 3). This decline in the amount of food consumed and assimilated by wild males may have been due to the presence of siblings competing for food, as 5 of the 6 males had siblings.

Dominance among sibling eagles is related to size, with the larger nestling dominating its sibling, particularly at mealtime (Meyburg 1974; Gargett 1978, 1982; Edwards and Collopy 1983; Bortolotti 1986). At the beginning of chick rearing, because of asynchronous hatching, the older nestling typically is dominant, regardless of sex. If the older chick is female it usually dominates its sibling throughout chick rearing. The size advantage associated with hatching first diminishes rapidly, however, if the older sibling is male and the younger is female. Three of the six wild male nestlings monitored in this study had female siblings. In two of these broods the male nestling was older and larger and maintained his dominance over the female chick until approximately the fifth week after hatching. Subsequently, the younger, but larger, female became more aggressive and frequently controlled access to the adult female during mealtime. Presumably, it was this shift in sibling interaction and dominance that caused the depressed ME values among wild males during subsequent weeks of chick rearing.

Recently, Bortolotti (1986) argued that eagle species vary in their patterns of growth, not because of sibling competition for food as proposed

by Werschkul and Jackson (1979), but because of selection to reduce peak energy requirements of nestlings. He also discussed how the growth of eagles in a food-limited situation can result in younger siblings growing at a slower rate. Among Bald Eagles (*Haliaeetus leucocephalus*) Bortolotti found that, regardless of the sex combination in the brood, younger siblings had lower growth rates ($K$), later inflection points ($t$), and equal asymptotic weights ($A$). He attributed these differences largely to the effects of asynchronous hatching and considered the slower growth of the younger chicks phenotypic.

My results suggest that the growth patterns of Golden Eagle nestlings also may be related to gender. In this study, wild male Golden Eagles had higher growth rates ($K$), earlier inflection points ($t$), and lower asymptotic weights. Sexual differences in growth patterns occur not only in Golden Eagles, but in seven of nine other species measured by Olendorff (1971). Newton (1979) also reported that in most dimorphic raptor species for which data are available, males fledge earlier than females. If sibling competition, as Bortolotti (1986) suggests, is not a major force in the selection of growth rates, then the sex-specific growth patterns seen among highly dimorphic raptor species should be examined more closely to determine their role in minimizing peak energy requirements.

## ACKNOWLEDGMENTS

This study was part of the Snake River Birds of Prey Research Project and was funded largely by the Bureau of Land Management. Partial funding also was provided by the National Wildlife Federation, Sigma Xi, and the University of Michigan. Many individuals assisted throughout this study; in particular, I thank D. McCullough, J. Diana, R. Drobney, A. Jensen, and R. Storer. M. Kochert, K. Steenhof, A. Bammann, and other BLM employees provided insight and valuable technical assistance. Special thanks go to T. Edwards and D. Blasdell for their dedicated field assistance and to K. Collopy for her skillful handling and care of the captive birds during the feeding experiments. Thanks also go to G. Duke and P. Rettig for advice on raptor care and nutrition. L. Oftedahl and G. Smith reliably collected the jack rabbits needed for the captive study. Laboratory analyses on the water, fat, and energy content of jack rabbit and eagle pellets and excrement were performed by J. Koplin, Humboldt State University and Hibbs Laboratories, Boise, Idaho, in 1978, and Standard Laboratories, Corbin, Kentucky, in 1979. R. Ricklefs graciously offered to fit curves to the eagle growth data using his computer programs. I also appreciate the critical reviews offered by S. Beissinger, K. Bildstein, G. Bortolotti, T. Edwards, J. Gessaman, M. Kochert, and K. Steenhof. This paper is contribution 5612 of the Journal Series, Florida Agricultural Experiment Station, Gainesville, Florida.

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# GENERAL NOTES

*Wilson Bull.*, 98(3), 1986, pp. 459–462

**Clutch-size differences in western and introduced eastern populations of House Finches: patterns and hypotheses.**—Factors influencing avian clutch size have been discussed by many workers (e.g., Lack 1954, Perrins 1965, Cody 1966, Skutch 1967, Ricklefs 1980, and references therein). Many of these observers have hypothesized that population density, or density relative to food supply can influence clutch size. When population density or population density relative to food supply is low, there should be more food available to raise young, and clutch sizes should be larger.

House Finches (*Carpodacus mexicanus*) are native to western North America from Mexico to British Columbia. An eastern population was established in New York City when cagebird dealers released House Finches in 1940 (Elliot and Arbib 1953). The released birds probably came from southern California (Elliot and Arbib 1953, Aldrich and Weske 1978). Bock and Lepthien (1976), and Bystrak and Robbins (1978) reported that the eastern House Finch population increased exponentially by a factor of 0.24/year during the 1960s through the early 1970s. Here, I examine differences in clutch size in eastern and western House Finch populations and detail how the differences relate to clutch size-specific fledging rates, predation rates, cowbird parasitism rates, and population density. I predicted that clutch size should be greater in the low-density eastern population, which is undergoing exponential growth in a previously unexploited area, because relatively more food would be available to finches there.

*Methods.*—I used data from the North American Nest Record Card Program (NRCP) conducted by the Cornell University Laboratory of Ornithology. In this program, volunteer observers record location, habitat, and nest history information on standardized cards. Cards are sent to the Cornell Laboratory of Ornithology for editing and computer storage. Peakall (1970) reviewed the NRCP and concluded that this program's clutch-size data are reliable, particularly with large sample sizes, despite the biases inherent in volunteer-based multi-observer programs.

I analyzed only those cards with completed clutches. These included cards with more than one observation of a particular clutch size, an observation of a clutch after the estimated last egg date, or an observation of the number of eggs and young at hatching time. Cards of nests that were deserted during incubation or that were parasitized by Brown-headed Cowbirds (*Molothrus ater*) were not included in clutch size comparisons, but were used in a separate analysis of the possible effects of interspecific competition on clutch size. Additional clutch data were taken from Gill and Lanyon (1965) and Bull (1974). In my analysis of fledging rates, clutch sizes were considered as the largest number of eggs or young reported on a card.

Clutch sizes in the presumed parent southern Californian population (nests inside a block from 33° to 35°40′N by 116° to 119°W) were compared to those in the eastern population (states to the north of North Carolina and east of Indiana). I tested for latitudinal effects by comparing both eastern and northwestern nests at the same latitude (above 36°45′N), and northwestern and southern Californian nests. All comparisons were made using one-tailed $t$-tests with pooled variance (Snedecor and Cochran 1980), as the hypotheses being examined all had a priori predictions. I estimated relative population density in the three areas using Breeding Bird Survey (BBS) data from the U.S. Fish and Wildlife Service. Any difference in density between eastern and western populations could be influenced in part by eastern observers unfamiliar with the introduced House Finches. However, House Finches have

TABLE 1
CLUTCH SIZES AND DENSITIES OF THREE POPULATIONS OF HOUSE FINCHES

| | East[a] | West | |
|---|---|---|---|
| | | Southern California | Northwest[b] |
| Density (birds/route)[c] | 0.29 | 42.44 | 17.20 |
| Mean clutch size | 4.53 ± 0.86 (108)[d] | 4.21 ± 0.87 (128) | 4.35 ± 0.84 (195) |

[a] Maine, Massachusetts, New Hampshire, Vermont, Ontario, New York, Connecticut, Rhode Island, Pennsylvania, New Jersey, Delaware, Virginia, West Virginia, Kentucky, Ohio, and Michigan.
[b] Northern California (>36°45′N), Oregon, and Washington.
[c] A route consists of 50 3-min counting locations at 0.8-km intervals.
[d] $\bar{x}$ ± SD (N).

now been in the East for more than 40 years, hence observer recognition is likely, and the BBS rigorously screens the quality of its observers, choosing experienced birders, who are likely to be familiar with House Finches (Robbins and VanVelzen 1967). To determine the influence of clutch size on fledging success, I compared clutch size-specific fledging rates (proportion of eggs fledged) of eastern and western nests using a $\chi^2$ test.

*Results and discussion.*—Results of NRCP analysis (Table 1) indicate that clutch size is significantly greater in the East than in southern California ($P = 0.002$), despite high variance caused by the discrete nature of clutch size. Several hypotheses might explain this greater clutch size. Clutch size might be greater in the Northeast than in southern California because of latitudinal differences (Lack 1954, Cody 1966, Ricklefs 1980). However, because clutch size in the Northwest was not significantly greater than in southern California ($P = 0.079$), and because it was significantly smaller than in the East ($P = 0.037$) (Table 1), latitude is an unlikely explanation for the difference in clutch size. A second possibility is that clutch size differences result from altitudinal variation (Lack 1954). A comparison of western clutches at different altitudes (<610 m, 610–1220 m, >1220 m), however, showed no significant difference (one-way ANOVA, $P = 0.25$).

A third possibility is that predation pressure or interspecific brood parasitism is higher in the West. First, increased clutch size could make nests easier to detect by predators or brood parasites because of an increased chance of spotting eggs, an increased chance that the young will be heard by a predator, or an increased chance of nest detection if more young require more feeding trips by adults. Several lines of evidence make this hypothesis unlikely. If anything, the proportion of eggs fledging increases overall with increased clutch size in both eastern and western nests (Table 2). Second, cowbird nest parasitism is significantly more common in eastern than in western nests (11 vs 1% of the nests, $P < 0.005$). Finally, cowbirds tended (N = 46) to lay in nests well before clutch completion, when clutch sizes were substantially smaller ($\bar{x} = 2.33 \pm 0.91$ [SD]) than completed southern California clutches ($P < 0.005$), suggesting that final clutch size plays little role in nest detection by cowbirds.

A second way predation, as well as catastrophic weather, might affect clutch size is by favoring birds who spread the risk. For example, in an area with a high predation rate, birds that conserve energy by reducing clutch size may be able to lay more eggs later in the nesting season if their first clutch is destroyed. To test this hypothesis, I compared the proportion of nests that failed completely (presumably a reflection of predation or some other extrinsic mortality factor rather than starvation) between the eastern and western finch populations. The proportion of eastern nests that failed completely (no fledged young) was significantly

TABLE 2

PERCENTAGE OF EGGS IN CLUTCHES OF EASTERN AND WESTERN HOUSE FINCHES THAT FLEDGED

| Clutch size | % Total eggs fledged (N) | | % Eggs fledged (N) in nests that fledged at least one young | |
|---|---|---|---|---|
| | East | West | East | West |
| 1 | 0 (1) | 0 (2) | — | — |
| 2 | 61 (18) | 50 (26) | 92 (12) | 93 (14) |
| 3 | 68 (123) | 59 (144) | 90 (93) | 89 (96) |
| 4 | 70 (528) | 66 (648) | 86 (428) | 86 (500) |
| 5 | 75 (500) | 63 (595) | 88 (425) | 86 (435) |
| ≥6 | 95 (19) | 65 (78) | 95 (19) | 77 (66) |

lower than that of western nests (54 of 286 vs 95 of 357, $P < 0.025$). This supports the spreading-the-risk hypothesis.

The East has a much lower density of House Finches in BBS counts (Table 1) than does the Northwest or southern California, consistent with the density hypothesis. Effects of density on clutch size could be direct, or could interact with food and other resource levels (Lack 1954, Ashmole 1963, Cody 1966, Ricklefs 1980).

After factoring out nests that failed completely, the proportion of eggs that successfully fledged was higher in the eastern population than in the western population for nests with three or more eggs (Table 2). When fledging rates are broken down into clutch size classes greater than and less than the mean clutch size, eastern nests have significantly higher fledging rates in 4-egg nests (binomial test, $P = 0.048$), but not in smaller clutches ($P = 0.37$). In larger clutches, western House Finches produce fewer offspring per energy investment than do eastern individuals (Table 2).

The relative importance of differences in population density and predation rates may be determined if the eastern population reaches equilibrium in the future. If larger clutches in the eastern House Finch result from lower population density, then as the population increases, clutch size should decrease. If the differences in clutch size are the result of differences in predation rates, cowbird parasitism, or other density-independent sources of nest loss, clutch size in the eastern population should remain at its present level.

A third possible explanation for the differences in clutch size is founder effect. This possibility is essentially untestable, although measurements of clutch size heritability might shed some light on its plausibility (Van Noordwijk et al. 1980).

In summary, House Finch clutch sizes are significantly higher in the introduced eastern population than in the native western population. These differences are not explained by differences in latitude or altitude, but may be the result of higher predation rates or population density in the West. Brown-headed Cowbird nest parasitism is higher in the eastern population, but it does not explain differences in clutch size. The difference in cowbird parasitism, which may be caused by a higher density of cowbirds in the East or by a difference in host species availability, merits further investigation. Further examination of clutch size, if the eastern population equilibrates, should shed more light on the relative importance of density and predation on clutch size.

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J. Timothy Wootton, *Dept. Zoology NJ-15, Univ. Washington, Seattle, Washington 98195.*
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**Late fledging dates, renesting, and large clutches of Prairie Falcons.**—Most reported hatching dates for Prairie Falcons (*Falco mexicanus*) are earlier than 17 June (Becker and Ball 1983). Late nesting and renesting across the species' range are not well documented, and their importance to resource managers needs to be elucidated. Here we present information on 14 nesting attempts with hatching dates of 12 June or later and discuss their importance.

Nesting surveys were conducted from 1973 through 1983 at the Birds of Prey Area (BPA) in southern Idaho (data from KS), in northeastern New Mexico in 1974 (SWP), in northeastern Colorado from 1976 through 1978 (SWP), in southwestern Wyoming from 1981 through 1984 (SWP), and in western North Dakota from 1982 through 1984 (GTA and RKM). Hatching dates were estimated by back-dating from the ages of nestlings or from observations of pipping eggs. Ages of nestlings were estimated at the times of aerie visits and by comparing photographs of nestlings to those in Moritsch (1983). We use "aerie" to mean a cavity in which Prairie Falcons nested or attempted to nest. "Nest site" refers to an aerie and its surroundings. There may be more than one aerie at a nest site, though each site is occupied by only one pair of Prairie Falcons in a nesting season.

During the 11-year study period at the BPA, 8 of 517 nesting attempts (1.5%) that could be dated reliably had hatching dates of 12 June or later (Table 1). Two of these were confirmed renesting attempts. We found no relationship between the occurrence of late nesting attempts at the BPA and temperature or precipitation during the time when incubation normally occurs (Kendall's tau, all $P > 0.05$), nor did we find any unusual nest-site characteristics common to the late nesting attempts.

We suspect, however, that 3 late nesting dates in North Dakota in 1984 (18% of the known nesting attempts in the state) represent renesting that followed a 26–27 April blizzard. GTA and RKM found 2 additional aeries in which nesting attempts failed, presumably due to wet and cold conditions during and just after the storm. Apparently, renesting was not attempted at either nest site. In one aerie, sand moved by melting snow flowed into the nesting scrape and partly buried the eggs. We are uncertain how the blizzard may have affected other aeries in which first nesting attempts failed, as they appeared undamaged by the storm. Perhaps male Prairie Falcons were unable to hunt successfully for several days, and females became less attentive and abandoned their nests. The storm likely promoted rapid chilling of eggs of all but the most attentive adults. Morrison and Walton (1980) indicated clutch replacement periods of 13–25 days for Prairie Falcons. The hatching dates at the 3 nest sites with apparent renesting attempts indicate that the adults could have renested and completed incubation by the time the sites were checked in late June and early July.

The largest clutch previously reported for Prairie Falcons is 6 eggs (Bent 1938). A clutch of 7 Prairie Falcon eggs was found at the BPA in 1978 in a nest used by Common Ravens (*Corvus corax*) in 1977. The 7 eggs were not believed to be the result of a renesting effort, and probably comprised a single large clutch. None of these eggs hatched.

The aerie with the latest hatching date in North Dakota in 1984 contained 7 eggs and one nestling on 8 July. There are at least four explanations for the large clutch. An adult falcon had appeared to be incubating in the aerie on 17 April and on 12 and 22 May, but we cannot be certain it was always the same bird. Therefore, a second female may have laid eggs in the aerie, either as a replacement female or in a nesting attempt coincidental with that of the first female. One female present at the site during the entire nesting season may have laid a replacement clutch of 8 eggs or she may have laid a replacement clutch among

TABLE 1
LATE NESTING ATTEMPTS BY PRAIRIE FALCONS, 1973–1984

| Hatching date | Fledging date[a] | Year | Outcome | Renesting attempt |
|---|---|---|---|---|
| | | Idaho (BPA) | | |
| 12 June | 20 July | 1978 | Failed | Yes |
| 14 June | 22 July | 1983 | Fledged | ? |
| 16 June | 24 July | 1980 | Failed | Yes |
| 18 June | 26 July | 1980 | Fledged | ? |
| 22 June | 30 July | 1974 | Failed | ? |
| 23 June | 31 July | 1974 | Failed | ? |
| 24 June | 1 Aug | 1981 | Unknown | ? |
| 29 June | 6 Aug | 1976 | Fledged | ? |
| | | New Mexico | | |
| 26 June | 3 Aug | 1974 | Fledged | ? |
| | | Wyoming | | |
| 16 June | 22 July | 1983 | Fledged[b] | ? |
| 30 June | 7 Aug[c] | 1983 | Fledged | Yes |
| | | North Dakota | | |
| 19 June | 27 July | 1984 | Fledged | Yes?[d] |
| 20 June | 28 July | 1984 | Fledged[e] | Yes?[d] |
| 6 July | 13 Aug | 1984 | Failed | Yes?[d] |

[a] Based on a mean 38-day nestling period observed at 92 aeries at the BPA with reliably estimated hatching and fledging dates.
[b] Nesting by a one-year-old female.
[c] Actual fledging date 12 August.
[d] See text.
[e] Based on behavior of adults on 5 August.

eggs that failed to hatch. We believe it is most likely that one female laid a replacement clutch in the aerie without removing her first clutch. The 6 eggs that remained in the aerie on 31 July were laid in 1984. We could not separate them into different sets based on markings, sizes, or contents. We found this aerie and a possible alternate in 1983, but we do not know if other suitable cavities were available. Although Tyler (1923) stated that the same aerie usually is used for renesting, we know of no other observations of aerie reuse in the same season.

SWP found an aerie in northeastern Colorado in 1977 in which a female was incubating 7 eggs. Three of the 7 eggs were dry, and probably had been in the aerie at least since the previous year. The 4 eggs from 1977 hatched, and 4 young fledged. Thus, it appears that a female Prairie Falcon may lay a new clutch among older eggs.

Wrege and Cade (1977) found that for captive Peregrine Falcons (*F. peregrinus*) egg laying was later for younger females. One-year-old birds comprised 33% of the breeding population of female Prairie Falcons captured in 1976 and 1977 in northeastern Colorado (Platt 1977). Juvenile females contributed 50% of the known recruitment in that study. In our study, we know only that one of the 2 females involved in the late nesting attempts in Wyoming in 1983 was a juvenile (Table 1). Late nesting in other areas also may be partly a result of nesting efforts by first year females.

The late nestings reported here for Idaho (1974 and 1980), Wyoming (1983), and North Dakota (1984) are the only instances known to us of more than one late nesting in an area in the same season. In Idaho, New Mexico, and Wyoming, late nesting appeared unrelated to the weather that prevailed during times when incubation normally occurs, and we did not find any unusual nest-site characteristics common to late nesting attempts. We suspect that the late nesting attempts in North Dakota were due to harsh weather earlier in the nesting season. Late nesting or renesting by Prairie Falcons apparently occurs throughout the range of the species. Renesting may be more common in years when spring weather causes first nesting attempts to fail. Therefore, late fledging also may occur more frequently than previously thought, particularly in the northern part of the range of the species. Eight (62%) of the late nesting attempts with known fates that we report here were successful. Projected fledging dates for the 14 nesting attempts, based on a 38-day nestling period, range from 20 July to 13 August (Table 1). Possible late nesting and renesting attempts and reuse of aeries in a single season should be considered when planning management of human activities near Prairie Falcon aeries.

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George T. Allen, *Zoology Dept., North Dakota State Univ., Fargo, North Dakota 58105*; Robert K. Murphy, *Lostwood National Wildlife Refuge, RR 2, Kenmare, North Dakota 58746*; Karen Steenhof, *Snake River Birds of Prey Research Project, Bureau of Land Management, 3948 Development Avenue, Boise, Idaho 83705*; and Stephen W. Platt, *2018 Reagan Avenue, Rock Springs, Wyoming 82901.* *Received 22 Jan. 1985, accepted 29 Jan. 1986.*

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**Characteristics of Red-shouldered Hawk nests in southeast Ohio.**—Studies have examined nest-site habitat of Red-shouldered Hawks (*Buteo lineatus*) in Iowa (Bednarz and Dinsmore 1981, Bednarz and Dinsmore 1982), Maryland (Titus and Mosher 1981), and southwestern Quebec (Morris et al. 1982, Morris and Lemon 1983). Red-shouldered Hawk (RSH) nesting habitat has not been studied extensively in Ohio, where the species is listed as potentially threatened (Ohio Dept. Natural Resources 1982). Here I describe the nesting habitat of RSH in southeastern Ohio, and compare habitat in Ohio with that used by this species in Maryland.

The 34-km$^2$ study area is mixed mesophytic forest (Braun 1961) in Hocking, Athens, and Vinton counties in the unglaciated Allegheny Plateau of southeastern Ohio. The area is characterized by deciduous forest, pine plantations, and strip mines. Topography ranges from 680 to 1010 m in elevation and is dissected by small rivers and streams. Riparian habitats are dominated by sycamore (*Platanus occidentalis*), American beech (*Fagus grandifolia*), silver maple (*Acer saccharinum*), and river birch (*Betula nigra*).

Active nest sites were found during March and April, 1979–1982, following the techniques of Craighead and Craighead (1956). Nest-site habitats were sampled during late summer 1983, using a variation of a standardized method for sampling raptor nesting habitat (J. Mosher, pers. comm.). Habitat variables were measured in 3 0.04-ha (11.3 m radius) circular plots. One plot was centered at the nest tree (nest plot) and the other 2 plots (satellite plots) were positioned randomly to the north and south or to the east and west of the nest. The distance between the center of the satellite plots and the nest tree was selected randomly between 1 and 75 m.

Twenty habitat variables were measured in nest plots and 15 variables were measured in satellite plots (Table 1). Canopy heights, nest-tree heights, and nest heights were measured by triangulation with a range finder. Distances from the center of the plot to the nearest permanent water and to the nearest forest opening (minimum size 100 m$^2$) were measured directly when $<100$ m, and they were measured on 7.5-min U.S.G.S. quadrangle topographic maps when $>100$ m. Percent canopy cover and percent understory cover were calculated from a total of 20 ocular tube sightings (James and Shugart 1970) for each measurement. Sightings were made along 2 perpendicular transects.

Paired $t$-tests (Freund 1971) were used to test for significant differences ($P < 0.05$) between the means of variables common to nest and satellite plots. The average values of the 2 satellite plots were used in these comparisons. Principal axis factoring with a varimax rotation (Harman 1967) was used to determine which variables best characterized nest-site habitat. I used Student's $t$-tests (Freund 1971) to compare nest-site characteristics of Ohio-nesting RSH with those nesting in Maryland.

Twelve of the 15 nests in the study were found in sycamore trees and one each was found in a tulip tree (*Liriodendron tulipifera*), a white oak (*Quercus alba*), and a river birch. Sycamore trees were used as a nest tree at a significantly higher proportion than other tree species of similar size (binomial test, $P < 0.01$).

Factor analysis revealed that 8 factors were important in characterizing RSH nest sites. The first factor accounted for 17% of the variation, and represented the number of trees with a DBH of less than 50 cm. Factor 2 explained 15% of the variation and represented nest height and percent nest height. The third and fourth factors explained 12% of the variation, respectively. Factor 3 represented trees with DBH greater than 50 cm and factor 4 represented distance to permanent water. Factor 5 explained 10% of the variation and represented canopy height and canopy cover. Factors 6, 7, and 8 together explained 28% of the variation and represented number of trees with DBH less than 50 cm and canopy height.

TABLE 1
HABITAT VARIABLES MEASURED AT STUDY PLOTS IN SOUTHEASTERN OHIO

| Variable mnemonic | Description |
|---|---|
| Variables measured only at nest plots | |
| ALTITUDE | Altitude of plot (m). |
| DBH | Diameter (cm) of nest tree at breast height. |
| NESTHT | Nest height (m). |
| HTNSTTRE | Nest tree height (m). |
| PNSTHT | Percentage nest height − (nest height/nest tree height) × (100). |
| Variables measured at all 3 plots[a] | |
| CANHT | Canopy height (m); average of 5 measurements of canopy height in each plot. |
| WATER | Distance (m) to nearest permanent water. |
| DISFOROP | Distance to nearest forest opening. |
| CANCOV | Percentage total canopy cover. |
| UNDCOV | Percentage total understory cover. |
| DBH 4–8 | Number of trees of 4–8 cm dbh in plot. |
| DBH 9–12 | Number of trees of 9–12 cm dbh in plot. |
| DBH 13–16 | Number of trees of 13–16 cm dbh in plot. |
| DBH 17–20 | Number of trees of 17–20 cm dbh in plot. |
| DBH 21–25 | Number of trees of 21–25 cm dbh in plot. |
| DBH 26–50 | Number of trees of 26–50 cm dbh in plot. |
| DBH >50 | Number of trees of >50 cm dbh in plot. |
| OVERTR | Number of overstory trees in plot. |
| UNDERTR | Number of understory trees in plot. |
| SHRUBDEN | Shrub density.[b] |

[a] The 3 plots include the nest plot and 2 satellite plots.
[b] See James and Shugart (1970) for details.

Although Red-shouldered Hawks frequently nest in trees that emerge from the canopy, percent nest height (60%) indicates that RSH placed their nests either in or slightly below the canopy. Morris et al. (1982) suggested that this nest placement may render the nest less visible to potential predators after the appearance of foliage. Nesting within the canopy may make nesting RSH less vulnerable to avian predators such as Great Horned Owls (*Bubo virginianus*).

Another selective advantage of nesting within the canopy may be moderation of the thermal environment of the nest (Ricklefs and Hainesworth 1969, Calder 1973). The moderation of the thermal environment may involve decreased wind velocity, and, as a consequence, decreased convective heat loss to the environment. Bednarz and Dinsmore (1982) have suggested that RSH may be forced to nest in the subcanopy because of a minimum branch size required to support the nest structure.

The importance of distance to nearest permanent water to breeding Ohio RSH may reflect the dietary habits of RSH, which include small rodents, birds, snakes, insects, and particularly amphibians.

Mean values of canopy height, canopy cover, understory cover, and number of trees with

TABLE 2

SAMPLE MEANS (± SD) AND PAIRED *t*-TEST VALUES FOR RED-SHOULDERED HAWK NEST SITES AND SATELLITE PLOTS IN SOUTHEASTERN OHIO

| Variable | Nest plot (N = 15) | Satellite plot (N = 15) | *t*-value |
|---|---|---|---|
| CANHT | 24.9 ± 7.3 | 18.9 ± 5.9 | 2.69[a] |
| WATER | 41.0 ± 77.8 | 50.1 ± 81.2 | 2.03 |
| DISFOROP | 20.0 ± 23.4 | 24.2 ± 32.9 | 0.05 |
| CANCOV | 84.0 ± 8.9 | 64.7 ± 20.9 | 2.91[a] |
| UNDCOV | 71.0 ± 14.1 | 57.0 ± 21.0 | 2.38[a] |
| DBH 4–8 | 11.8 ± 9.5 | 14.2 ± 8.4 | 0.54 |
| DBH 9–12 | 4.6 ± 3.0 | 5.4 ± 3.4 | 0.78 |
| DBH 13–16 | 3.2 ± 2.0 | 3.0 ± 1.5 | 0.32 |
| DBH 17–20 | 1.9 ± 1.4 | 1.9 ± 1.6 | 0.09 |
| DBH 21–25 | 1.6 ± 1.5 | 1.7 ± 1.3 | 0.30 |
| DBH 26–50 | 3.6 ± 2.6 | 2.7 ± 1.5 | 1.60 |
| DBH >50 | 2.0 ± 1.4 | 0.6 ± 0.7 | 3.61[b] |
| OVERTR | 4.6 ± 2.3 | 6.4 ± 3.4 | 1.58 |
| UNDERTR | 24.8 ± 14.0 | 23.2 ± 12.8 | 0.41 |
| SHRUBDEN | 27.9 ± 28.0 | 29.1 ± 21.4 | 0.18 |

[a] $P < 0.05$ using a paired *t*-test.
[b] $P < 0.01$ using a paired *t*-test.

DBH greater than 50 cm were significantly greater for the nest plots (Table 2) than for the satellite plots. Greater canopy height and percent canopy cover were associated with the greater number of overstory trees with DBH greater than 50 cm in the nest plots, indicating that RSH nesting habitat was not homogeneous.

Comparison of common habitat variables in Ohio and Maryland using Student's *t*-tests revealed that distance to forest opening was significantly greater ($P < 0.01$) in Maryland. Percent canopy cover and number of trees with DBH greater than 50 cm were significantly greater in Ohio ($P < 0.05$). The greater distance to forest opening in Maryland probably reflects a difference in study sites. The Maryland study site is extensively forested. The Ohio study site is characterized by small residential communities, primary roads, secondary roads, and large wood lots. Large contiguous forested tracts in southeastern Ohio typically occur only along rivers and streams.

This study indicates that Ohio RSH place their nests in mature riparian forests where they use large diameter trees for nesting and have large open hunting areas in close proximity.

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MARK S. WOODREY, *Dept. Zoology, The Ohio State Univ., Columbus, Ohio 43210.* *Received 24 Sept. 1984, accepted 5 Mar. 1986.*

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**Sprig delivery by Broad-winged Hawks.**—Adults of many species of nest-building Falconiformes place fresh green sprigs on their stick nests (Wimberger 1984). Although numerous functions for greenery on nests have been proposed (Olendorff 1971, Newton 1979), there are few published accounts of sprig delivery, and these records are based primarily on incidental observations. This report provides details of sprig delivery by Broad-winged Hawks (*Buteo platypterus*), and supplements previous observations (Burns 1911, Matray 1974, Bush and Gehlbach 1978, Rosenfield 1982).

*Methods.*—The study was conducted during the 1981 and 1982 breeding seasons in Allegany and Garrett counties, Maryland. Study sites and Broad-winged Hawk nest-site habitat are described in Titus and Mosher (1981).

We used a 15–60× spotting scope, and monitored sprig deliveries from blinds at three nests from 11 days posthatch until nestlings first left the nest (31–33 days). Hatch dates (±24 h) were known at one nest, and an age-estimation model (Lyons and Mosher 1983) was used to determine the age of nestlings at two nests. Observation periods of 275 min were randomly prescheduled between 06:00–21:00.

We distinguished individuals of a mated pair either by the presence of blue dye on breast feathers or by naturally occurring plumage characteristics. The sex of birds was determined by comparing observed parental behavior with that described by Matray (1974), who sexed trapped birds according to the presence or absence of a brood patch.

In addition to these observations, eight nest trees each were climbed from 1–12 times (47 total visits) from late incubation to fledging in 1981, and the presence of fresh greenery in nests was recorded. Twelve different nests each were visited 1–13 times (66 total visits) over

the same period in 1982. When fresh greenery was present we recorded species of sprig tree and percent of the nest cup covered by fresh greenery. Sprigs were designated "fresh" if leaves were green and could be folded without creasing or breaking. Nest observations were made by DML.

*Results and discussion.*—Fresh sprigs were observed at 39 of 47 (83%) and 49 of 66 (74%) of the nest visits in 1981 and 1982, respectively. Only one of 20 nests did not contain greenery, and this nest was visited only once. At six nests (visited both before and after hatching) the percent of the nest cup covered by fresh greenery during the 2-week period after all eggs hatched ($\bar{x}$ = 59 ± 8 [SE]) was not significantly greater (one-tailed sign test, $P$ = 0.344) than that observed in the last 2 weeks of incubation ($\bar{x}$ = 43 ± 17).

Twenty-four posthatch sprig deliveries were recorded at three nests that were watched for a total of 128.3 h (28 observation periods). Adult females made all 24 sprig deliveries, as well as 14 of 18 posthatch deliveries of leafless twigs. This is in accord with observations that females are primarily responsible for nest construction by raptors (Olendorff 1971).

Sprig delivery rates did not change appreciably until 26 days posthatch, when delivery rates abruptly declined. We encountered very little fresh greenery in nest visits during the fourth week, when old accumulated greenery was as deep as 5–7 cm in the center of some nests. The decline in sprig delivery was associated with a decline in adult female attentiveness at nests. By the fourth week, the young were feeding themselves, and parents remained at nests for only brief periods to deposit food. Nestlings fought over food at this time and frequently pursued adults returning to the nest. The risk of injury during encounters with young at the nest (Jenkins 1978) may have inhibited sprig delivery during this period.

Prior to 26 days posthatch, seven sprigs were delivered in 36.6 h of observation from 06:00–11:00 (0.19 sprigs/h), 14 sprigs were delivered in 34.9 h of observation from 11:00–16:00 (0.40 sprigs/h), and one was delivered in 20.2 h of observation from 16:00–21:00 (0.05 sprigs/h). Thus, approximately 3.2 sprigs were delivered to a nest per day. If this daily rate continued from hatching to 26 days posthatch, an average of 83.2 sprigs would be delivered to a nest during the nestling period. Matray (1974) counted 65 and 54 sprigs in two nests at four weeks posthatch.

Sprigs from six species of trees were found in a total of 49 visits to 11 nests in 1982. Most nests contained sprigs from two to four species, although on seven consecutive visits, one nest contained only black locust (*Robinia pseudoacacia*) sprigs. Burns (1911) stated that only one species of sprig was used in individual nests, but Matray (1974) reported as many as five species in a single nest.

Twice we observed sprig collection by one adult. The female grasped a sprig in her beak while perched on a branch, tugged it free, and carried it to the nest in her beak. Both collection sites were in overstory trees within 25 m of the nest.

Birds usually placed greenery on the nest rim or cup with little effort to incorporate sprigs into the nest. Most sprigs were simply dropped on the nest, but birds sometimes spent several minutes moving sprigs about in their beaks. Occasionally a sprig was dropped on top of nestlings. Previous observers have suggested that sprig delivery serves to hide nestlings from predators (Criddle 1917) or to shade nestlings from the sun (Bush and Gehlbach 1978). Nestlings, however, were partially covered by sprigs in only 4 of 24 deliveries we observed.

We observed small amounts of greenery in partially completed hawk nests shortly after onset of nest construction. The nest-sanitation hypothesis (Orians and Kuhlman 1956) does not explain the presence of greenery in nests during this period of the breeding season. Similarly, territorial advertisement (Newton 1979) is an insufficient explanation for sprig delivery as greenery is delivered to nests containing eggs or nestlings, which readily indicate territorial occupancy.

Clark and Mason (1984) presented empirical evidence supporting an ectoparasite-repellent

function (Wimberger 1984) for nest greenery. Our observations suggest an additional function. Decaying greenery fills gaps between twigs, consolidates the nest structure, and may lengthen the period during which a nest remains in a tree (Newton 1979). Greenery use is significantly correlated with nest reuse in Falconiformes (Wimberger 1984). A long-term nest maintenance function would be useful to birds that reused nests in successive years as they may spend less time and energy refurbishing an old nest structure, and could begin laying eggs earlier than pairs that build entirely new nests. Early egg-laying pairs generally have greater reproductive success (Newton 1979).

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David M. Lyons, Kimberly Titus, and James A. Mosher, *Appalachian Environmental Lab., Univ. Maryland, Center for Environmental and Estuarine Studies, Frostburg State College Campus, Gunter Hall, Frostburg, Maryland 21532.* (Present address DML: *Animal Behavior Graduate Group, Dept. Animal Science, Univ. California, Davis, California 95616.*)
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**Reverse mounting in the American Kestrel.**—Reverse mounting during mating has been reported in a number of avian orders (see James 1983 for review). Several authors imply that the behavior is aberrant (Ficken 1963, Nolan 1978, Thompson and Lanyon 1979), while others suggest that reverse mounting is a normal behavioral trait during courtship (Glick 1954, Kilham 1961, Nuechterlein and Storer 1982). James (1983) suggests that the behavior may be designed to obtain the full cooperation of a mate during courtship or after a nest failure. Here we report two instances of reverse mounting in free-ranging American Kestrels (*Falco sparverius*), the first recorded for Falconiformes, between females and the males that replaced their original mates after they were experimentally removed.

During 1983 and 1984, in southwestern Quebec, one member of each of 20 mated kestrel pairs was removed from the wild and the remaining bird was color banded. We removed the mate of female C84 on 26 May 1984. She continued incubating her clutch and, on 7 June, engaged in normal courtship and copulation with a new unmarked male. On 9 June the pair disappeared from the territory. Upon inspection we removed 4 addled eggs from the box. On 12 June the new male returned and repeatedly inspected the available nest box. At 16:35 of the same day, both male and female were preening within 100 m of the nest box. The male leaned forward, a typical female precursor to copulation (Willoughby and Cade 1964), and the female mounted him in typical copulatory posture (Balgooyen 1976) for approximately 5 sec. The birds preened side by side for 45 sec, and the female flew to and entered the nest box. Within 15 min the male copulated with the female.

In the second instance, we removed the mate of female H84 on 25 May 1984. A new male was observed on the territory within 18 h, and the pair immediately began courting, even though H84 continued to incubate the original clutch. On 27 May the male entered the nest box, but later that day the pair abandoned the territory. When we examined the nest box we found shell fragments from the freshly destroyed clutch. Within 2 days the pair returned to the territory, and the male inspected the nest box. At 14:10 on 6 June the male flew from the nest box and preened about 5 m above the box. At 14:20 the female landed next to the male. The male leaned forward, and the female mounted him for 3 sec. They preened for 1 min; then the female leaned forward, and the male mounted her. In neither instance of reverse mounting was actual cloacal contact observed.

James (1983) suggested that reverse mounting by the female may be a stronger than usual signal to re-stimulate her mate for a replacement nest. Females may also need a strong stimulus to renest. Of 8 female kestrels who, having lost their original mate, received a replacement, only 4 subsequently laid a second clutch (Bowman 1985). Of these, 2 pairs were observed reverse mounting. All kestrels laying clutches late in the season, including replacement pairs, have significantly lower nesting success (Bowman 1985); a stronger than usual signal may be helpful to stimulate renesting.

Though reverse mounting has not been previously described as part of normal courtship in kestrels, there are few intensive observational studies of early courtship in wild birds. Mounting has been associated with the establishment of dominance in mammals (Maslow 1940) and birds (Fujioka and Yamagishi 1981).

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REED BOWMAN AND ELIZABETH M. CURLEY, *Macdonald Raptor Research Centre, Macdonald College of McGill Univ., 21,111 Lakeshore Rd., Ste.-Anne-de Bellevue, Quebec H9X 1C0, Canada.* (Present address RB: *Dept. Wildlife and Range Sciences, Univ. Florida, Gainesville, Florida 32611*; EMC: *121 Miles Ave., Syracuse, New York 13210.*) *Received 22 Aug. 1985, accepted 24 Jan. 1986.*

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**Intraspecific brood parasitism in three species of prairie-breeding shorebirds.**—Intraspecific brood parasitism has been reported in fewer than 100 avian species (Yom-Tov 1980). For precocial birds it is common among ratites, phasianids, and, particularly, anatids (Andersson 1984). Shorebirds are characterized by small, fixed clutch sizes, and abnormally large clutches are uncommon (Cramp and Simmons 1983). Intra- and interspecific egg-dumping account for many of these large clutches. Other instances result when more than one female contributes to the laying and care of combined clutches (Walters and Walters 1980). Here I document three shorebird nests that each contained eggs from more than one female of the same species.

The three nests included those of a Western Willet (*Catoptrophorus semipalmatus*), a Marbled Godwit (*Limosa fedoa*), and a Wilson's Phalarope (*Phalaropus tricolor*) at Last Mountain Lake Wildlife Management Unit in southcentral Saskatchewan. From 1982 to 1985, when I studied shorebirds in the area, water conditions changed dramatically. All observed cases of brood parasitism occurred in 1984, a year of severe drought in which 75% of local wetlands were dry. The severity of the drought reduced available breeding sites for

TABLE 1
DENSITY OF PAIRS OF SHOREBIRDS AT TWO SITES IN SOUTHCENTRAL SASKATCHEWAN FROM 1982 TO 1985

| Species | Ephemeral wetland | | | | Permanent wetland[b] | |
|---|---|---|---|---|---|---|
| | 1982 | 1983[a] | 1984[a] | 1985 | 1984 | 1985 |
| Killdeer | 10 | 7 | 1 | 12 | 10 | 5 |
| American Avocet | 8 | 0 | 0 | 25 | 8 | 1 |
| Western Willet | 3 | 2 | 0 | 5 | 5 | 3 |
| Spotted Sandpiper | 0 | 0 | 0 | 0 | 3 | 2 |
| Upland Sandpiper | 2 | 1 | 1 | 2 | 4 | 3 |
| Marbled Godwit | 5 | 1 | 1 | 5 | 7 | 4 |
| Common Snipe | 0 | 0 | 0 | 0 | 3 | 2 |
| Wilson's Phalarope[c] | 45 | 20 | 0 | 30 | 55 | 80 |

[a] Wetland was dry during most (1983) or all (1984) of the breeding season.
[b] Incompletely censused in 1982 and 1983.
[c] Densities are of nesting males, as this species is occasionally polyandrous (Colwell, in press).

several species of shorebirds, and the few remaining wetlands supported high densities of breeding pairs (Table 1).

Each year, I monitored nesting pairs of all shorebird species to obtain accurate egg-laying chronologies. During the four years, I found 336 nests of nine species (109 nests in 1984), including nests of 3 Piping Plovers (*Charadrius melodus*), 38 Killdeers (*C. vociferus*), 35 American Avocets (*Recurvirostra americana*), 8 Western Willets, a Spotted Sandpiper (*Actitis macularia*), 2 Upland Sandpipers (*Bartramia longicauda*), 14 Marbled Godwits, 3 Common Snipes (*Gallinago gallinago*), and 232 Wilson's Phalaropes. The following observations describe the three instances of brood parasitism I observed.

*Observations.*—On 7 May 1984 I found an unlined scrape of a Western Willet that contained one egg. A 4-egg clutch was completed late on 12 May or early on 13 May. When I next visited the nest on 22 May, it held a fifth, distinctly differently colored egg. No additional eggs were laid. Both adults were color banded. The pair hatched two chicks from the initial four eggs on 7 June and lost the remaining three eggs to a predator on the same day. As the laying date for the fifth egg was unknown, I cannot be certain that it was laid by a second female. However, the egg's unique color suggests that it was.

Between 5 and 10 May, a color-banded pair of Marbled Godwits performed courtship scraping on their territory. One of their scrapes contained three eggs on 14 May. The 4-egg clutch was completed on 15 May. During the morning of 22 May the nest held a fifth egg. Two more eggs were laid on 23 and 24 May. Shortly thereafter the 7-egg clutch was destroyed by an unknown predator. Another, unbanded godwit pair initiated a clutch less than 300 m away on 18 May. The first egg in this nest was taken by a predator, suggesting that the three eggs deposited in the parasitized nest could have belonged to this female.

During the afternoon of 26 June, I flushed an unbanded male Wilson's Phalarope from a nest that contained three eggs. On the morning of 27 June the nest held four eggs, and that afternoon it contained five eggs. The morning of 28 June a sixth egg was laid. Sometime between 13:00 and 14:15, on the same day, a seventh egg was laid in the nest. No additional eggs were laid and the male deserted the clutch at that time. The laying of five eggs in less than 76 hours indicates that at least two females laid the eggs. The male's breeding rela-

tionship to the females was unknown. It may have been that two pairs were using the same nest as has been recorded for other shorebirds (Cramp and Simmons 1983).

*Discussion.*—Andersson (1984) discussed two evolutionary routes that favor brood parasitism among precocial birds. The limited breeding-site hypothesis suggests that brood parasitism occurs when a shortage of breeding opportunities forces two females to lay in the same nest. Selection would favor this behavior if one female subsequently obtained another breeding site that allowed her to produce additional offspring. The predation hypothesis states that nest failure prior to clutch completion leads females to parasitize nests because they possess fertilized eggs that need to be laid. The common occurrence of nest parasitism among ground nesters that suffer high levels of predation supports this hypothesis (Andersson 1984).

For prairie-breeding shorebirds, ecological conditions promoting nest parasitism may occur during drought years when breeding sites are limited, predation is high, and brood parasites can readily locate nests in habitats with high nest densities. For all shorebirds, nest loss to predators was highest during the dry years of 1983 and 1984 ($G = 39.4$, df = 3, $P < 0.001$).

Perhaps the most important biological features restricting nest parasitism among shorebirds are small clutch size and daily laying interval (Andersson 1984). Together, they impose strict limits of synchrony between the parasite's and host's reproductive cycles. Failure to lay eggs during the host's laying period may result in eggs hatching asynchronously and therefore being deserted. Other precocial birds that commonly parasitize nests are characterized by large clutch sizes allowing for a greater window of vulnerability to parasitism (Andersson 1984).

Although brood parasitism may not be common in shorebirds, I suggest that its occurrence may be linked to ecological conditions that restrict breeding opportunities and, at the same time, increase levels of predation.

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Mark A. Colwell, *Biology Dept., Univ. North Dakota, Grand Forks, North Dakota 58202.*
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**Suspected intraspecific egg dumping in the White Ibis (*Eudocimus albus*).**—Bird colonies may present a favorable environment for brood parasitism, as large numbers of synchronously nesting conspecifics are available as potential hosts (Hamilton and Orians 1965, Payne 1977). *Intra*specific nest parasitism (i.e., egg dumping), however, has been reported in only a handful of colonially nesting birds (Yom-Tov 1980; Fox and Boersma 1983; Brown 1984; Fetterolf and Blokpoel 1984; Emlen and Wrege 1986). Cannell and Harrington (1984) reported *inter*specific nest parasitism by a Great Egret (*Casmerodius albus*) and Black-crowned Night-Herons (*Nycticorax nycticorax*) at a mixed-species heronry and suggested that a low level of inter- and intraspecific nest parasitism may exist in wading birds (Ciconiiformes). A single presumed instance of nest parasitism by a Maguari Stork (*Euxenura maguari*) reported by Thomas (1984) is, to our knowledge, the only published account of *intra*specific nest parasitism in the Ciconiiformes. Here we provide evidence of the occurrence of this behavior in White Ibises (*Eudocimus albus*).

We studied White Ibises at 2 colonies. Battery Island is a 40-ha National Audubon Society sanctuary near the mouth of the Cape Fear River, Brunswick County, North Carolina (33°54′N, 78°01′W), where ibises nest in a 7-ha maritime shrub thicket (Shields 1985). Peak nest numbers were 3737 in 1983 and 4849 in 1984. Pumpkinseed Island is an 8.9-ha colony in Winyah Bay, Georgetown County, South Carolina (33°16′N, 79°12′W), where ibises nest on a dense mat of black needlerush (*Juncus roemarianus*) (Frederick 1985). Peak nest numbers were 7814 in 1982 and 10,035 in 1983.

At Battery Island, 262 ibis nests in 1983 and 493 nests in 1984 were examined every 3–4 days from the onset of egg laying until chicks left their nests. Eggs were individually marked with indelible ink. At Pumpkinseed Island, 42 nests in 1982 and 71 in 1983 were checked (eggs counted, but not marked) at 10:00 every day from the onset of nest building through the apparent completion of clutches (more than three consecutive days without new eggs). Over 15,500 pair-hours of intensive observation from a blind were performed on Pumpkinseed during the egg-laying period.

Nest parasitism was never witnessed during these observations. We did, however, obtain circumstantial evidence of parasitism based on deviations from a normal egg-laying schedule. White Ibises usually lay eggs every other day (Bent 1926, Rudegeair 1975), and lay from two to four eggs in a clutch. Their eggs are easily distinguished from those of other species nesting on the two study sites. Three types of evidence of nest parasitism were obtained: (1) two eggs appearing in a nest on the same day, (2) a new egg appearing in a nest on each of two consecutive days, and (3) new eggs appearing after apparent clutch completion.

On Battery Island, nest checks were too infrequent to detect type 1 and 2 evidence, but type 3 evidence was noted twice in 1983 and 6 times in 1984. The mean interval between presumed clutch completion and the appearance of the suspected parasitic eggs was 11.7 ± 4.8 days [SD]. None of the apparently parasitic eggs hatched, probably because they had an incomplete incubation period. On Pumpkinseed Island, one case of type 2 evidence was found in 1982, and two cases each of type 1 and 2 evidence were noted in 1983. No type 3 cases were detected on Pumpkinseed, as nests there were not checked after apparent clutch completion. The fates of parasitic eggs on Pumpkinseed were not followed, but these eggs would have had normal incubation periods.

Because no birds are known to lay more than one egg in a single 24-h period (Sturkie 1965), type 1 evidence is the most conclusive circumstantial evidence of nest parasitism. Type 2 cases may represent instances in which nest owners laid eggs in a shorter than usual interval. However, if nest parasitism did occur, type 1 and 2 evidence should have been noted in roughly equal proportions unless the laying periods of hosts and parasites were

always exactly synchronous. Type 3 evidence could be interpreted as nest owners laying late eggs. However, the long time span between the apparent completion of clutches and the appearance of the late eggs indicates that these cases reprcsent instances of nest parasitism. The appearance of late eggs in nests at Battery Island was not preceded by egg loss, thus ruling out the possibility that the late eggs were replacements.

The evidence from both colonies suggests that a low level of intraspecific nest parasitism occurs in the White Ibis. Parasitic females did not always seem to be aware of the hosts' egg-laying period as the parasitic eggs detected at Battery Island were laid far too late to be incubated adequately by the hosts.

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Peter C. Frederick, *Dept. Biology, Univ. North Carolina, Chapel Hill, North Carolina 27514*; and Mark A. Shields, *Dept. Biological Sciences, Univ. North Carolina at Wil-*

*mington, Wilmington, North Carolina 28403.* (Present address PCF: *Dept. Wildlife and Range Science, Univ. Florida, Gainesville, Florida 32611*; MAS: *Wyoming Cooperative Fish and Wildlife Research Unit, Univ. Wyoming, Laramie, Wyoming 82071.*) *Received 26 Sept. 1985, accepted 5 Mar. 1986.*

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**A case of brood mixing by Common Loons.**—Common Loons (*Gavia immer*) are strongly territorial when rearing chicks (McIntyre 1975), and there is only one previous report of brood mixing in this species. Eckstein (1980) reported the successful fostering of a Common Loon chick by a pair with their own chick after a second chick was introduced by humans. We report here the details of a natural case of brood mixing by Common Loons.

In 1984, we monitored 16 territorial pairs of Common Loons on three lakes in northern Maine during nesting and chick rearing. On 1 and 2 August, RS observed a 3-chick brood in the traditionally used nursery area of the Boody Cove (BC) pair on Grand Lake Seboeis. The nest had 2 eggs and on 25 July, 2 chicks were seen. The 2 adjacent pairs, Coomb's Cove (CC) and Wadleigh Cove (WC), also had 2-egg nests that hatched successfully. On 25 July, one chick was present in WC and 2 were in CC. On 1 August, there were 2 chicks in CC, 3 in BC, and none in WC. The brood in BC was reduced to 2 chicks by 4 August and to one by 6 August. The CC brood remained at 2 chicks and none were seen in WC after 25 July.

All 3 BC chicks followed the attending adult as it swam slowly in the nursery area. The other adult was absent during observations on both days. We estimated the chicks to be 1–2 weeks old based on hatching dates, size, and plumage characteristics. We observed no aggression among the chicks or between the chicks and the adult. One of the chicks was seen riding on the adult's back on 1 August.

The chronology of chick numbers in adjacent territories suggests that a chick from the WC territory moved into the BC nursery area. The nurseries of the 2 territories were separated by 3 km, an extreme movement for a young loon. The WC chick may have been blown across the lake by the wind (cf. Sjolander and Agren 1976) or may have followed the adults during a territorial encounter and wandered into BC. There were no human residents on the lake and we do not believe the chick was moved by humans.

Common Loons should experience strong selection against acceptance of chicks from other broods because there is little possibility of relatedness. The probability of brood mixing, however, is low due to distances between nurseries (McIntyre 1983), limited movements of chicks, and strong territorial defense; and there has probably been little opportunity for natural selection to operate on chick recognition. Other gaviids also accept strange chicks (Abraham 1978, Dymond 1982).

To our knowledge, this is the first published report of natural brood mixing by Common Loons. We believe brood mixing is an unusual occurrence for gaviids and that acceptance of chicks is facilitated by a lack of selection pressure on chick recognition.

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PAUL I. V. STRONG, *240 Nutting Hall, Univ. Maine at Orono, Orono, Maine 04469*; JOHN A. BISSONETTE, *Maine Cooperative Wildlife Research Unit, 240 Nutting Hall, Univ. Maine at Orono, Orono, Maine 04469*; AND RICHARD SOUZA, *1139 Sarah Sherman Road, Rochester, Massachusetts 02770.* (Present address PIVS: *Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806*; JAB: *Utah Cooperative Fish and Wildlife Research Unit, Utah State Univ., Logan, Utah 84322.*) *Received 13 Nov. 1985, accepted 3 Feb. 1986.*

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**Use of fencepost cavities by nesting Eastern Bluebirds in southwestern Virginia.**—Fencepost cavities are often mentioned as providing suitable nest cavities for Eastern Bluebirds (*Sialia sialis*) (Hegner 1899, Howell 1932, Zeleny 1976). Relatively little information, however, exists on Eastern Bluebirds nesting in natural cavities, as distinct from nest boxes or other artificial nest cavities. Exceptions are data from tree cavities reported by Conner and Adkisson (1974) and Pinkowski (1974, 1976). We report on the use of fencepost cavities as nest sites in the rural farmlands surrounding Blacksburg, Virginia, and on the dimensions of those cavities.

*Study area and methods.*—The study area lies within the Ridge and Valley Province, with elevations from 550–760 m. The general pattern of land use consists of wooded, sparsely settled ridgetops, with cleared pastures and farmlands in the valleys, along the floodplains, and along the lower slopes.

During the breeding seasons of 1976 and 1977, Eastern Bluebird nests in fencepost cavities were found by driving roads in rural areas and searching for adult bluebirds on utility wires or fencerows. Once adults were spotted they were observed until we determined presence or location of the nest cavity. We also searched fencerows on foot for nest cavities. (However, when bluebirds were present in an area their vocalizations and their perching in open areas made them conspicuous.) All nests were within 32 km of Blacksburg.

Measurements of nest cavities were made after the breeding season in 1977. Nest material was removed from the cavity before interior dimensions were taken. Measurements included (1) height of the cavity entrance, the distance from the ground to the bottom of the cavity entrance; (2) entrance diameter, the average of the vertical and horizontal dimensions of the cavity entrance; (3) interior diameter, the average of four measurements, two taken at the cavity entrance and two taken at the cavity bottom; and (4) cavity depth, the distance from the bottom of the cavity entrance to the cavity bottom. Cavity volume was calculated from interior dimensions.

Means of cavity dimensions were tested for significance using the Mann-Whitney *U*-test (Blalock 1979).

*Results and discussion.*—Thirty-five nests of Eastern Bluebirds in fencepost cavities were found (Table 1). Other nests found in fencepost cavities included those of European Starlings

TABLE 1

DIMENSIONS OF FENCEPOST CAVITIES USED BY EASTERN BLUEBIRDS AND EUROPEAN STARLINGS IN SOUTHWESTERN VIRGINIA, 1976–1977

| | Mean ± SE (N) [range] | | | |
|---|---|---|---|---|
| | Eastern Bluebird | | European Starling | |
| Cavity height (cm) | 133.6 ± 3.8[a] | (35) [78.9–181.3] | 96.8 ± 11.1 | (6) [64.0–122.4] |
| Entrance diameter (cm) | 4.8 ± 0.3[b] | (35) [3.4–11.0] | 5.7 ± 0.4 | (6) [4.4–6.8] |
| Interior diameter (cm) | 7.7 ± 0.2[b] | (33) [5.8–11.9] | 10.0 ± 1.2 | (4) [7.4–13.0] |
| Cavity depth (cm) | 16.1 ± 1.0[c] | (33) [6.8–35.0] | 31.6 ± 3.3 | (6) [24.5–46.7] |
| Cavity volume ($cm^2$) | 808.4 ± 99.2[a] | (33) [252.4–2736.3] | 2572.5 ± 496.5 | (4) [1680.2–3919.0] |

[a] Probability of significant difference between means using Mann-Whitney *U*-test, $P < 0.01$.
[b] Probability of significant difference between means using Mann-Whitney *U*-test, $P < 0.05$.
[c] Probability of significant difference between means using Mann-Whitney *U*-test, $P < 0.001$.

(*Sturnus vulgaris*) (6), Carolina Chickadees (*Parus carolinensis*) (1), House Wrens (*Troglodytes aedon*) (1), and Northern Flickers (*Colaptes auratus*) (1).

Pinkowski (1976) considered the minimum cavity depth observed in his study to be a critical minimum below which the cavity was unacceptable for Eastern Bluebirds. One fencepost cavity observed in this study, however, had a depth of 6.8 cm, 0.8 cm less than the minimum reported by Pinkowski (1976). Cavity depth may influence nesting success, with shallower nest cavities being more susceptible to predation. Indeed, the nesting attempt in the shallowest fencepost cavity failed due to predation. On the other hand, an even shallower tree cavity in this study (Pierson 1978), which had a depth of 5.2 cm, was successful.

One fencepost cavity observed in this study had an entrance diameter of 3.4 cm, 0.3 cm less than the minimum reported by Pinkowski (1976). The female at this site struggled somewhat while entering the cavity, which appeared to be close to the minimum diameter usable by Eastern Bluebirds.

European Starlings nested in fencepost cavities that had significantly larger entrance diameters, larger interior dimensions, and were closer to the ground than those used by Eastern Bluebirds (Table 1).

Thirty-two (91%) Eastern Bluebird fencepost nest cavities studied were excavated by woodpeckers, having a more or less circular entrance hole in the side of the fencepost; three (8%) were produced by natural decay, having entrances to the nest cavity from the top of the post. Fenceposts with nest cavities were probably 30–40 years old. Age and natural decay in some fenceposts had advanced to the point that some fenceposts had a side entrance originally excavated by woodpeckers, as well as an opening at the top. Others had vertical gaps along the grain of the wood, and still others had small (0.4–3.0 cm diameter) holes in the portion of the post containing the nest cavity.

Two fenceposts that contained nest cavities were replaced with new wooden posts between the two breeding seasons; the top of a third post collapsed due to decay and was not used for nesting in 1977. No new cavities made by woodpeckers were discovered during the study. Thirty fenceposts that had cavities in 1976–77 were reinspected in 1983. Of the 30, between 6 and 10 were still usable. Seven of the original fenceposts had been replaced; ten posts had decayed to the point that a cavity no longer existed; two cavities were obscured by vegetation; and a house had been built near another fencepost cavity. Dennis (1969) reported an average longevity for Northern Flicker nest cavities of two or three years, with a maximum of nine years for a fencepost cavity.

*Conclusions.*—Fenceposts in rural farmlands such as those surrounding Blacksburg, Virginia, can provide suitable nest cavities for Eastern Bluebirds. Conner and Adkisson (1974) recommended that standing dead snags be left in clearcuts to provide nesting cavities for Eastern Bluebirds. We recommend that steps be taken to assure the availability of fencepost nest cavities. In light of our results, we urge that landowners allow old fenceposts containing nest cavities to remain standing and to buttress them with a new, sturdier post.

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THOMAS A. PIERSON AND PATRICK F. SCANLON, *Dept. Fisheries and Wildlife, Virginia Polytechnic Institute and State Univ., Blacksburg, Virginia 24061.* (Present address TAP: *13813 Cabernet Court, Chantilly, Virginia 22021.*) *Received 28 Oct. 1985, accepted 30 Jan. 1986.*

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**Little Blue Herons nesting among cattails.**—Little Blue Herons (*Egretta caerulea*) are known to nest in willow (*Salix* spp.), cypress (*Taxodium* spp.), mangrove (*Rhizophora* spp.), buttonbush (*Cephalanthus* spp.), and bamboo (*Smilax* spp.) (Bent 1926, Meanley 1955, Palmer 1962, Hancock and Elliott 1978). Burger (1978) recorded Little Blue Herons nesting in poison ivy bushes (*Rhus toxicodendron*), and Rodgers (1980) reported Little Blue Herons nesting in Brazilian pepper (*Schinus terebinthifolius*), cabbage palm (*Sabal palmetto*), black mangrove (*Avicennia germinans*), mulberry (*Morus rubra*), gray nicker (*Caesalpina crista*), marsh elder (*Iva frutescens*), and white mangrove (*Laguncularia racemosa*). This paper is the first report of Little Blue Herons nesting among cattails (*Typha domingensis*), an herbaceous vegetation. Burger (1974) reported Black-crowned Night Herons (*Nycticorax nycticorax*) nesting among cattails in northwestern Minnesota.

On 1 May 1985 I observed Little Blue Herons nesting on an 1130-ha reservoir at the Savannah River Plant in Barnwell County, South Carolina. The heronry was in a dense stand of emergent cattails in 1–2 m of water, 45 m from a stand of mainly loblolly pine (*Pinus taeda*). The cattail stand was approximately 20 × 15 m, with emergent leaves about 2 m high. Nests were constructed of small hardwood twigs laid less than 1 m above the water on the top of dead, flattened cattails. Cattail leaves around the margins of each nest may have been used to stabilize the nests. Leaves were not used in linings of nests. Burger (1978) reported Little Blue Herons nesting in *Rhus* bushes less than 1 m above ground in New Jersey. The 25–30 Little Blue Heron nests were spaced about 1–2 m from each other. Similar distances between nests have been recorded by Burger (1978) and Wiese (1978). On 1 May most nests contained 3–5 eggs. No nestlings were observed on 16 May, but by 31 May, 3–4 chicks were observed at most nests.

The herons may have nested in cattails because of climatic conditions. During the first 6 months of 1985, westcentral South Carolina received 20 cm less rainfall than normal. An island herony dominated by willow 500 m to the southwest of this site had no nesting in 1981, 1982, and 1985, all low water years. During these years, lower water levels at the reservoir may have made nests at the willow herony more accessible to terrestrial mammals, thus resulting in a movement of the herons to a more desirable location over deeper water.

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RICHARD T. HOPPE AND ROBERT A. KENNAMER, *Drawer E, Savannah River Ecology Laboratory, Aiken, South Carolina 29801.* (Present address RTH: *Indiana Dept. Nat. Res., Wildl. Manage.-North, RR4, Box 47, Peru, Indiana 46970.*) *Received 21 Oct. 1985, accepted 30 Jan. 1986.*

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**Swallows taking insects from pond surfaces.**—The abundance of flying insects is strongly affected by weather (Williams 1961, Taylor 1963); hence, it should be adaptive for birds that are primarily aerial insectivores to have alternative foraging strategies for times when flying insects are scarce. Early in this century, Forbush (1929) claimed that in early spring, Tree Swallows (*Tachycineta bicolor*) in New England left their breeding areas in cold windy weather and went to sheltered places "where the sun shines more warmly—where they can still find insects or can pick benumbed ones from the water or ice along the shore." Recently, Erskine (1984) reported observations of Tree Swallows and Violet-green Swallows (*T. thalassina*) foraging on the ground and cited other reports of Tree Swallows, Purple Martins (*Progne subis*), and Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) foraging on the ground and from ice surfaces. One of us (RRC) recently observed Tree Swallows taking active winter stoneflies (Plecoptera) from the surface of frozen ponds. King (1958, 1967) reported Barn Swallows (*Hirundo rustica*), Common House-Martins (*Delichon urbica*), and a Bank Swallow (*Riparia riparia*) taking dormant winged insects from the surface of the sea along the coast of England. We could find no published accounts of North American swallows taking benumbed or dead insects from water surfaces. Here we describe two such events that occurred in 1983 and 1984 near Denver, Colorado, during cold weather in the spring.

Mild weather prevailed in Colorado during 8–10 May 1983, with the air temperature in Denver reaching 27°C on 9 May (Denver Local Climatological Data, U.S. Dept. Commerce, 1983). The temperature did not exceed 5°C on 11 May, although it rose to 18°C on 12 May, only to drop again as a storm (rain, snow, and high wind) passed through the area on 13 and 14 May. From 16:00 to 17:00 on 14 May, MLD observed a mixed-species flock of swallows flying rapidly back and forth, close to the surface of Windsor Lake, a 25-ha pond

in southeastern Denver County. The flock included about 70 Barn Swallows, 35 Violet-green Swallows, 15 Cliff Swallows (*H. pyrrhonota*), 5 Bank Swallows, and 5 Tree Swallows. The birds frequently contacted the water surface with their beaks, as if picking small objects from the water. The water surface was littered with dead or moribund Diptera, apparently midges (Chironomidae), about 6 mm in body length. The air temperature was 5°C and the sky was overcast; there was little or no wind.

In 1984, mild weather prevailed in the Denver area on 16 and 17 April, with the air temperature reaching 24°C on 17 April, followed by a cold period with temperatures not exceeding 13°C on 18 April. From 08:30 to 10:00 on 19 April, Cohen observed this same food source and swallow feeding behavior in a flock of swallows at Cottonwood Marsh, a 7-ha pond in Walden Ponds County Park in eastern Boulder County. The flock included about 200 Tree Swallows, 50 Barn Swallows, 10 Violet-green Swallows, 10 Bank Swallows, and 5 Cliff Swallows. The sky was mostly cloudy with patches of fog, the air temperature ranged from 6 to 9°C. There was a 9-km/h N to NE wind. The birds' frequent contact with the surface again was clearly the type of action that swallows use to pick up small objects and unlike the action they use to drink from a water surface (Cohen, pers. obs.). Flying insects appeared to be scarce, and swallows did not appear to be foraging in the air as well as at the pond surface.

Swallows are commonly seen flying low over water surfaces in the early spring, perhaps foraging on active newly emergent insects (Erskine, pers. comm.). The observations reported here suggest that the taking of dead or moribund insects from water surfaces during cold weather may be a more common foraging behavior in swallows than has previously been recognized.

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Robert R. Cohen, *Dept. Biology, Box 53, Metropolitan State College, 1006 11th St., Denver, Colorado 80204*; and Mark L. Dymerski, *919 Elm St., Denver, Colorado 80220.*
*Received 30 Apr. 1985, accepted 31 Jan. 1986.*

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**Drinking by Northern Bobwhites in Texas.**—In the Southeast (Stoddard 1931) and western Oklahoma (Davison 1949), Northern Bobwhites (*Colinus virginianus*) apparently obtain sufficient moisture from preformed water and dew and rarely drink free water. In Texas, however, 468 bobwhites have been observed drinking at an earthen reservoir between 7:00 and 9:00 on a single day during drought (Lehmann 1984). We studied the drinking behavior of bobwhites at two sites in southern Texas to clarify questions about their use of surface water.

*Study sites and methods.*—Data were collected in Texas on the Welder Wildlife Refuge, San Patricio County, and the Encino Division of the King Ranch, Brooks County, from April 1984 through March 1985. At each site, a blind was established within 10 m of an earthen reservoir. Observation periods were from 0.5 h before sunrise to 11:00, 11:01 to 15:00, and 15:01 to 0.5 h after sunset. Each reservoir was observed twice monthly during morning and evening and once or twice monthly during midday. Observation periods lasted 1–6 h. When bobwhites visited a reservoir, we recorded their number and used a stopwatch to determine time spent in sight of water and drinking. Observations totaled 157 h at Welder and 166 h at Encino.

*Results.*—No bobwhites were observed at the Welder site. At the Encino site, a total of 27 quail visits was recorded on 14 occasions during 142 h of observation from 4 May–2 October. Birds spent 179 ± 28 sec [SE] (N = 14) near water. Drinking was recorded only during July (9), August (1), and October (2). Quail that drank visited water singly or in pairs during July through August; a covey of 9 drank in October. Drinking time averaged 58 ± 8 sec (N = 12). Twenty-one visits were between 1.5–2.5 h after sunrise and 6 were between 4–1.5 h before sunset.

*Discussion.*—Our failure to observe birds at the Welder site may have occurred because quail density was lower there (10 birds/40 ha vs 50–80 birds/40 ha at Encino [unpubl. data]), because drinking by gallinaceous birds in arid areas is associated with low availability of succulent foods (Elder 1956, Crawford and Bolen 1973, Degen et al. 1984), or both. During the time bobwhites were seen drinking, rainfall was 54 cm at Welder and 22 cm at Encino; respective mean maximum temperatures were 33.0 and 33.8°C. Presumably, dew and foods rich in preformed water were available in greater quantities at Welder than at Encino.

Different environments may also explain the difference in drinking behavior between bobwhites in the Southeast (Stoddard 1931) and Texas (Lehmann 1984, this study). Whereas annual precipitation exceeds 100 cm in much southeastern quail range, less than 60 cm falls about 36% of the time in southwestern quail range (Norwine and Bingham 1985). During the warmer months, particularly in drought years, preformed water is largely unavailable. Oxidative water does not appear to meet the needs of birds in drier environments (Bartholomew and Cade 1963). Our data indicate that when preformed water is limited and higher temperatures elevate the need for evaporative cooling, bobwhites in the warmer portions of Texas apparently drink surface water to supplement oxidative water.

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N. L. N. S. PRASAD AND FRED S. GUTHERY, *Caesar Kleberg Wildlife Research Institute, Texas A&I Univ., Kingsville, Texas 78363.* *Received 23 Nov. 1985, accepted 13 Feb. 1986.*

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**Severe aggression between female Black-headed Grosbeaks.**—On 27 May 1985 at 11:00, while conducting a study of the breeding biology of a color-banded population of Black-headed Grosbeaks (*Pheucticus melanocephalus*) in the Sandia Mountains in central New Mexico, I encountered two color-marked female grosbeaks engaged in a vigorous struggle. The birds were on the ground with their bills locked. At least one of the combatants continually emitted a loud distress call. As I watched, the bird on top (GRAO) forced its opponent (AORO) into a small stream but did not submerge the lower bird's head. GRAO had a nest with two eggs, one and 2 days from hatching, about 20 m from where the struggle took place. I did not know the breeding status of AORO, but I had seen it frequently about 300 m from the encounter. I observed the struggling birds for about 5 min before they moved into an area of very thick ground cover and disappeared from view.

The next day, AORO was captured in a trap 50 m from the location of the fight. The bird had several lacerations about its bill and throat and was bleeding from the mouth. It weighed 46.0 g, 5.0 g less than it had 2 weeks before. Despite its injuries, the bird flew off when released. On the night of 28–29 May a dog retrieved the body of AORO, which I believe almost certainly had died from injuries sustained in the struggle a day and a half earlier. An autopsy of the body revealed no injury that a dog might inflict (e.g., tooth marks or broken bones) but did show blood in the trachea and damage to the neck region coinciding with the wounds that were present when the bird was captured alive on the previous day. GRAO was trapped 3 days after the struggle and showed no signs of the battle. It was incubating eggs 3 h after the fight and both young in its nest fledged.

Intraspecific struggles resulting in death are rare even among male passerines (Lack 1956, Brown 1977, and references therein); however, Gowaty (1981, 1985) recently reported that female Eastern Bluebirds (*Sialia sialis*) frequently engage in vigorous clashes and occasionally kill one another. She hypothesized that fights between female bluebirds center around nest cavities, which are critical to reproduction but are limited in supply. Cavity owners may

fight to retain their nest sites while intruders may seek to oust owners or dump eggs into nests.

As in bluebirds, female-female aggression is a conspicuous aspect of the reproductive behavior of Black-headed Grosbeaks (Weston 1947, Ritchison 1983, pers. obs.). The circumstances leading to female aggression in Black-headed Grosbeaks, however, appear to be somewhat different than in bluebirds. Female grosbeaks build open cup nests in a number of species of small trees or shrubs, which are abundant on the study site. AORO had no mature or maturing ova in its oviduct when it died, and the eggs of GRAO had been incubated for 9 days and were close to hatching when the struggle took place. It therefore seems unlikely that the females were fighting for a nest site or that the intruding female was attempting to dump eggs. The females may have been fighting for access to a territorial male.

Black-headed Grosbeaks are strictly monogamous (Weston 1947, Ritchison 1983, pers. obs.). Although all (or nearly all) adult-plumaged male grosbeaks (males in their second breeding season or older) hold a territory and breed, very few subadult male grosbeaks (males in their first breeding season) do so (Ritchison 1980, pers. obs.). In contrast, yearling females are fully mature and commonly breed (pers. obs.). This leads to a potential surplus of reproductive females and a shortage of adult territorial males. My mist-netting data indicate that, while the ratio of all males to females is close to unity (1.12:1.00, N = 309, $\chi^2 = 0.94$, df = 1, $P > 0.30$), the ratio of adult males to females is 0.71:1.00 (N = 250, $\chi^2 = 7.06$, df = 1, $P < 0.01$).

Heightened female aggression has been noted in other species where territorial males are a valuable resource (e.g., Tree Swallows [*Tachycineta bicolor*] [Leffelaar and Robertson 1985] and woodpeckers [*Picoides, Melanerpes, Sphyrapicus*] [Lawrence 1967, Kilham 1983]). I propose that populations of monogamous passerines with a surplus of reproductive females may not be as rare as has been supposed (Brown 1968), and that such a situation may explain the high degree of aggression displayed by females of many species of passerine, including Black-headed Grosbeaks.

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GEOFFREY E. HILL, *Dept. Biology, Univ. New Mexico, Albuquerque, New Mexico 87131.* (Present address: *Museum of Zoology and Div. Biological Sciences, Univ. Michigan, Ann Arbor, Michigan 48109.*) *Received 20 Nov. 1985, accepted 4 Mar. 1986.*

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**An albino Greater Shearwater: feather abrasion and flight energetics.**—Barrowclough and Sibley (1980) speculated on the survival potential of a partially albinistic Yellow-rumped Warbler (*Dendroica coronata*) whose white flight feathers were severely abraded. As they pointed out, the actual significance of increased abrasion to albinistic flight feathers remains uncertain for two reasons: (1) the relationship of fitness to flight energetics is unknown and (2) the importance of other factors (e.g., camouflage and countershading) needs to be evaluated.

Previous authors (e.g., Averill 1923) observed that black shows less wear than white on primary feathers, and Voitkevich (1966) suggested that the presence of melanin was associated with increased thickness of keratin in these same feathers. The importance of melanin was confirmed by experimental abrasion of differently colored and pigmented warbler feathers (Burtt 1979). Barrowclough and Sibley (1980), however, argue the significance of abrasion-resistant coloration among wild birds.

On 28 August 1980, 40 miles SE of Oregon Inlet, Dare County, North Carolina (30°30′N 74°38′W) DSL observed and collected an albinistic Greater Shearwater (*Puffinus gravis*) from a mixed feeding flock of 30–40 Greater and Cory's Shearwaters (*Calonectris diomedea*).

At a range of 30 m, the bird appeared to lack the maneuverability, speed, and grace of the shearwaters with which it was associated. Although other shearwaters nearby soared on very light winds, the albino flapped and generally remained 3–5 m above conspecifics. Unlike the other individuals it never landed on the water to feed and its wing beat appeared faster and deeper.

The bird, a female (NCSM 7741; ovary 3.5 × 8.0 mm) weighed 424.3 g. The iris was dark brown. The bill was flesh colored, lighter than that of a normal Greater Shearwater, and the tarsi and feet were light pink with the outer toe of each foot gray-brown. All plumage was essentially unpigmented, except for faintly dark coloration in feathers of the "cap," tail, and spotting on the tips of the primary wing coverts and on feathers on the leading, ventral surface of the wings. All feathers were old and very worn. The tail and flight feathers were abraded to the extent that the wings were abnormally shortened and on the remaining distal 5 cm of most primary feathers the barbs were lacking. Microscopic examination revealed that most distal barbs, when present, lacked barbules. We assume this resulted from abrasion.

Most of the collected Greater Shearwaters found lingering off the North Carolina coast during the summer months (10-year study, see Lee and Booth 1979) are young birds. Timing of molt suggests the albino Greater Shearwater was almost certainly immature and probably a yearling. That this individual showed no sign of feather replacement even by late August when most immature birds have advanced molt may indicate its poor general condition. As prefledgling Greater Shearwaters spend about 3 months in nest burrows, feather abrasion may have begun before the bird could fly.

Compared to 18 normally pigmented Greater Shearwaters collected in the same area (666.0 ± 98.2 g [SD]) the 424.3 g weight of the albino specimen was low. When we compared various measurements that relate to flight, the albino was well below similar measurements for birds with normal abrasion. Measurable percent of difference was recorded for wing span (−8.2), wing chord (−3.6), and tail length (−6.4). The total wing area of the albino (as calculated by tracing the outline of the outstretched wings on paper) was 10.8% smaller than the average area of normally pigmented specimens.

The emaciated condition of the albino bird resulted in a lower wing-loading ratio (0.53 $g/cm^2$) than for normally pigmented birds with typical feather abrasion (0.75 $g/cm^2$, assuming an average weight of 666.0 g). A bird of normal weight with a wing surface area of the albino specimen, however, would have a wing-loading ratio of 0.84 $g/cm^2$ (12% higher loading). If the distal 5 cm of the primaries are not included in the wing area a truer picture of the labored flight energetics can be obtained. These figures reveal a total effective wing area of 738 $cm^2$ (17.1% less than that of a normally pigmented bird) and a wing-loading ratio of 0.58 $g/cm^2$ and one of 0.90 $g/cm^2$ for a bird of average weight.

Like most Procellariidae, Greater Shearwaters forage over pelagic regions where prey is distributed in discontinuous and sporadically available patches. Sustained economical flight is therefore critical to survival. The feather abrasion on this bird clearly placed it at a disadvantage. In fact, the 5 Greater Shearwaters we salvaged in June 1984, after a small die off, were in starved condition and weighed 372 (range = 337–432) g. These weights closely agree with that of the albino.

This represents only the second record known to us (see Alexander 1898) of a shearwater in which the degree of albinism was extensive, and one of only a few reports of extensive albinism in Procellariiformes. Our report demonstrates how increased abrasion may affect fitness and provides support for the long held belief that pigment in flight feathers contributes both to the lack of deterioration of feathers and ultimately to the potential for survival of the bird. Other factors related to feather pigment, such as loss of camouflage and counter-shading (Barrowclough and Sibley 1980), would not seem critical to survival in large shearwaters.

*Acknowledgments.*—W. Irvin and S. P. Platania (NCSM) accompanied Lee on the trip in which the albino bird was collected. Irvin prepared the specimen and made some of the descriptive notes on which this manuscript is based. R. C. Laybourne (USNM) examined the bird and confirmed our identification. The study is an outgrowth of a comprehensive offshore study funded by the U.S. Fish and Wildlife Laboratory, Slidell (Louisiana) Laboratory (Contract #92375-1130-621-16). E. H. Burtt, Jr. provided many helpful comments on this paper.

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DAVID S. LEE AND GILBERT S. GRANT, *North Carolina State Museum of Natural History, P.O. Box 27647, Raleigh, North Carolina 27611.* *Received 30 Nov. 1985, accepted 5 March 1986.*

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# ORNITHOLOGICAL LITERATURE

CONSERVATION OF TROPICAL FOREST BIRDS. A. W. Diamond and T. E. Lovejoy (eds.). ICBP Technical Publ. No. 4, 1985:318 pp. £18.50.—This book presents the proceedings of a workshop and symposium held at the XVIII World Conference of the International Council for Bird Preservation on 7, 8, and 10 August 1982 in Cambridge, England. Numbers 2 and 3 in ICBP's Technical Publication series, on the conservation of seabirds and island birds, respectively, arose from the same conference. All are available postpaid from ICBP, 219c Huntingdon Rd., Cambridge CB3 0DL, England.

ICBP's symposium on the conservation of tropical forest birds drew 21 written contributions from ornithologists around the world. Coverage, extensive but not complete, was strongest for Middle America, Colombia, Brazil, all of Africa except Madagascar, and southeast Asia except India, Sri Lanka, and the Philippines. Symposium convenor A. W. Diamond noted in his preface that the symposium is intended to promote knowledge of the roles played by birds in tropical forest ecosystems, to identify tropical forest areas where birds are at risk, and to promote conservation of suitable forest areas to ensure survival of bird species.

The book is in four parts. The first part, entitled "Global Perspectives," begins with an overview of tropical rain forest bird ecology and evolution by Allen Keast. A. W. Diamond summarizes tropical forest bird distribution patterns, the conservation implications of identifying and conserving centers of endemism and areas of species richness (CORE areas), and an appraisal of current efforts to measure the rate of depletion of tropical forests. Not only are we unable to measure this loss with any satisfying degree of accuracy, but the existing global network of reserves and parks is woefully inadequate in preserving tropical forest CORE areas. F. G. Stiles gives us a solid pragmatic reason for preserving tropical forest birds: in neotropical forests up to three-quarters or more of tree seed dispersal is accomplished by birds.

Part Two deals with the status of tropical forest birds in the New World. Summary assessment by D. W. Snow that Colombia and southeastern Brazil contain the greatest numbers of threatened species relative to the extent of forest destruction is followed by survey papers by M. A. Ramos on Mexico and Central America, F. S. Delgado B. on Panama, J. E. Orejuela on Colombia, D. A. Scott and M. deL. Brooke on southeastern Brazil, and F. G. Stiles on Costa Rica.

Part Three covers the Paleotropics. Africa is ably and thoroughly covered by J. M. Thiollay (west), S. N. Stuart (east), and R. J. Dowsett (central and southern). D. R. Wells surveys the bulk of southeast Asia, excluding the Philippines. B. Beehler treats the problems of New Guinea, suggesting that forest preservation there should be based on a series of reserves protecting birds of paradise, species that have ritual significance and recognition value to the people of New Guinea. M. Wong presents a case study of the effects of logging and regeneration on birds in a Malaysian rain forest. Many forest birds return quickly as rain forest regenerates, as long as cutting is selective and nearby mature patches provide colonization sources.

Part Four presents the proceedings of the workshop, which preceded the symposium. The separation of the workshop papers from those of the symposium in this volume seems artificial, for the nature of 5 of the 6 papers in this part complements papers in the preceding 2 parts, while extending coverage to Australia and Western Samoa. Unique in this part is a presentation, compiled by A. W. Diamond, summing the themes arising from the workshop that are common to tropical forest bird conservation around the globe: the nature and

relative importance of the threats; the crucial locations where attention should focus most urgently; and the actions ICBP might undertake to address the problem, namely, preparation of atlases of distribution of tropical forest birds from which centers of endemism and species diversity can be identified. The latter should lead to decisions on the establishment and protection of reserves that take into account the requirements of tropical forest birds, including those that move between habitats, altitudes, regions, or seasons.

The book tells us that some tropical forests are far more valuable than others from an ornithologist's viewpoint. Similar information on CORE areas of taxonomic groups other than birds is still lacking or is quite incomplete, but when assembled it will help to guide choices by those protecting forest land. The rub is that time is running out. In the interval between this symposium and publication of the proceedings, 600,000 $km^2$ of tropical forest, roughly 6% of the total, was seriously altered or destroyed. Lowland forests will largely be gone in the Philippines, peninsular Malaysia, and much of West Africa and Central America by 1990. We are learning which pieces of forest to save at the same time we are losing the option to choose. At risk here and now is much of the 30% of the world's avifauna that inhabit tropical forests, as well as the forests themselves, with which these birds have coevolved. This situation is the most significant, most compelling topic in ornithology today. In this book for the first time the problem, which no ornithologist can ignore, is addressed on a global basis, area by area, and species by species.—WARREN B. KING.

BOBWHITES IN THE RIO GRANDE PLAIN OF TEXAS. By Val W. Lehmann, with illustrations by Nancy McGowan. Texas A&M Univ. Press, College Station, Texas 1984:371 pp., 45 figs., 9 color plates. $20.00 (cloth).—This is not an easy book to digest in one reading as it includes an abundance of data. It represents a lifetime of study by Val Lehmann, undoubtedly the most knowledgeable person working with Northern Bobwhites (*Colinus virginianus*), over the last 4 decades. The book is organized into 3 parts: Life History (22 chapters), Management Considerations (12 chapters), and Management Recommendations (11 chapters). It also contains 11 appendixes, Literature Cited, and a useful index.

The presentation of the text, figures, and plates is attractive, and the organization is logical. However, the text is not well-edited and some redundancy occurs, especially in parts II and III. I found no typographical errors, although it should be Ellisor (1975a) on p. 77 (not Ellisor [1975]). The amount of wasted space throughout the book is enormous (see especially pp. 144–145, 238–240, 308–310).

Some chapters are short (2 pp., chapters 36 and 39) while others are apparently long enough to warrant a summary (chapters 10, 21, 45). This inconsistency also includes the use of English and metric units. Most measures are in English units (pp. 61, 62, and elsewhere), but on p. 151 weights are given in grams, while in Table 31.6 and on p. 273 both grams and pounds are used. Most figures add to and support the text although some do not (Plates 2.2, 2.3, 2.4). Others: plate 13.5 showing remains of turkeys killed by hail, 16.2 of a coyote den, 16.10 of a coyote scat, 33.2 of Wild Turkeys (*Meleagris gallopavo*), and the bottom color photo on p. 33, add little to the text and could be omitted. The same is true for some tables (especially 29.1 on the fate of turkey nests, 29.3 on the contents of 100 Harris Hawk [*Parabuteo unicinctus*] stomachs, and 29.4 on the contents of 66 Greater Roadrunner [*Geococcyx californianus*] stomachs) and the discussion on turkeys and deer (pp. 194–195), coyote poisoning (pp. 193–194), cotton rats (pp. 210–214), and relationships of bobwhites with other species (Chapter 33).

At times the writing is abrupt with incomplete sentences (pp. 46, 102) and the reader is introduced to new words ("eventuated," p. 38; "chickhood," p. 111; "hatchability," p. 112; "survivability," p. 113; "withal," p. 113; "shootable," p. 245) or strange uses of words

("personnel transfer" for movements between covies, pp. 51, 331, 342; "weaned" for independent young, pp. 45, 115; "aged" for classification of age, pp. 85, 195–196; "stomachs" instead of crops, tables 25–1, 2, and 4; "weeds" instead of forbs, pp. 172–174, 179, 296, 321–322, 352–355). Such words as "always" (pp. 49, 82, 110, 257) and "never" (pp. 16, 199, 318) are also used when the data are not definitive. The author also fails to define "heavy soils" (p. 16), "just right conditions" (p. 16), "good years" (p. 27), and "judicious grazing" (caption for color plate on p. 112, p. 164). Scaled Quail (*Callipepla squamata*) are referred to as "blues" (pp. 19, 141, 222, 224, 226–230, 305), and there is one figure (33.1), 3 plates (33.3, 4b, 5), and a lengthy discussion (pp. 222–230) on this species.

While data are presented throughout the book, there also are unsupported statements (pp. 11, 15, 27, 92, 135, 303–304, and elsewhere) and speculation (chapters 13, 18). Statistical treatment of data is almost nonexistent, although the data sets are more than adequate for this type of rigorous testing. It would be especially desirable to test the validity of the car bush census (pp. 19–21) where 95% accuracy is claimed. The author's interpretation of some data sets may not be the same as the readers', especially in chapters 4, 6, 10, 13, 19, and 22, and Appendix C.

Lehmann obviously has data on the impacts of livestock grazing on quail at all seasons of the year under most environmental conditions. However, he avoids extensive discussion of livestock grazing, although the reader obtains the impression that the author has severe reservations about this cultural practice (see especially color plate on p. 112). Measures of the results of management practices (Part III) are apparently nonexistent as no data are presented. Despite this problem, the section on Management Recommendations contains many practical suggestions on how to manage lands for bobwhites (and other wildlife).

The appendixes are useful even though bird names (Appendix A) do not follow the American Ornithologists' Union, mammal names do not follow the American Society of Mammalogists, and no sources were given for the names of amphibians, reptiles, and invertebrates (Appendix A). I also question the inclusion of 1980–82 data on chick food habits when all other food habits data are from 1933–35. The appendixes on parasites (I, J) are overdone, as only 13 of 41 external parasites were reported from Texas, and the taxonomic descriptions of helminth parasites are unwarranted. I also question the inclusion of quail hunting records (Appendix K) from the Nilo Plantation in Illinois. Finally, although the Rosene and Lay (1963) citation is included in the Literature Cited, I could not find where it was used in the text.

Despite these criticisms, "Bobwhites in the Rio Grande Plain of Texas" is recommended for serious students of quail, land managers, and those of us who are interested in the natural history of birds. Val Lehmann is to be commended for drawing together the knowledge and data that he has accumulated on this species over the last 40+ years. Too often, too many of us are data collectors and amass observations that are not adequately massaged and published. Val Lehmann is thanked for reminding us that we do have an obligation to make our data available to our peers. This book is a steal at $20.00.—CLAIT E. BRAUN.

BIRD BEHAVIOR. By Robert Burton. Bruce Campbell (Consulting Editor). Alfred A. Knopf, New York, New York, 1985:224 pp., 600 color photographs. $18.95.—Despite increasing interest in birds by the general public, few books present the findings of ethologists in a nontechnical manner. The gap has now been filled by this attractive, readable, and informative book. Most major aspects of avian behavior are covered. The chapters are: The Living Bird, Flight, Senses and Intelligence, Finding Food, Diet and Way of Life, Communication, Social Life, Courtship and Mating, Rearing of Young, and Migration.

The unifying theme of the text is the adaptiveness of behavior, including cost-benefit

analysis of flight patterns, migration, social behavior, etc. Such an evolutionary approach is unusual in a book for a general audience, but the emphasis makes it much more interesting than a presentation consisting solely of various "tidbits" of behavior. Even ornithologists will probably find some new information. For example, we are informed that swiftlets (*Collacalia* spp.) carry nest material in their feet so that they can echolocate, that the young of Oilbirds (*Steatornis caripensis*) take 100 days to fledge (they can afford this development, slow even for a frugivore, because of reduced predation associated with cave-nesting), and that "milk" is not just given to the young of pigeons, but also to Emperor Penguins (*Aptenodytes forsteri*) and flamingos. In addition to presenting results of many descriptive studies, numerous experiments are described (such as tests of the Beau Geste hypothesis), another unusual feature of a "popular" bird book.

In seeking readability by a general audience, some authors succumb to liberal use of anthropomorphic statements. Only a few are found here. Sunbathing is described as "enjoyable" and "more than a functional pursuit" and avian communication is "often extremely sophisticated, more so than immediately seems to be necessary. . ." Statements such as these are rare exceptions in a book that is outstanding in its scientific approach.

The book is unusual in its breadth of coverage. It is concerned with the behavior of the birds of the world, rather than using only North American and European examples. The book seems remarkably free of errors. The photograph on p. 169 is mislabeled as that of a "Bushtit", although it is a Long-tailed Tit (*Aegithalos caudatus*). Common names are used in the text and photo captions, but the index provides scientific names.

Most of the photographs are not only beautiful, but an integral part of the book, enhancing the text, and showing the behavior of a variety of species. Some series of photographs are particularly outstanding in their presentation of behavior: aggression and courtship at a Ruff (*Philomachus pugnax*) lek, an Egyptian vulture (*Neophron percnopterus*) opening an Ostrich (*Struthio camelus*) egg with a stone, a Green-backed Heron (*Butorides virescens*) fishing with "bait," to name a few. In addition to effective use of a series of pictures to show behavioral events, many individual pictures are especially memorable. My favorites are a Red-backed Hawk (*Buteo polyosoma*) with its head cocked to one side as it flies (obviously scanning), triple exposure of a Tawny Owl (*Strix aluco*) showing how its head moves from side to side to judge distance, a Fairy Tern (*Gygis alba*) having laid an egg on a branch where it would normally be safe sitting unperturbed next to a skink and a Toc Toc Bird (*Foudia seychellarum*) that is eating the egg, and an African Jacana (*Actophilornis africana*) walking while carrying a young tucked under its wing. In a book with so many photographs used to demonstrate behavior, it is not surprising that some are of poor quality, and a few are questionable choices as they are so small that the birds appear as tiny dots. Despite these minor flaws, the book succeeds in presenting not just a remarkable collection of photographs of perched or flying birds, as is the usual case, but of birds engaged in a variety of behavioral activities.

This is a book that can be read and enjoyed by all. It might even be appropriate for use as an adjunct text in an ornithology course. "Bird Behavior" should inspire many to a greater appreciation of why birds behave the way they do. At $18.95 it is also a bargain.—MILLICENT S. FICKEN.

USE OF SNAGS BY CAVITY-NESTING BIRDS IN THE SIERRA NEVADA. By Martin G. Raphael and Marshall White. Wildlife Monographs No. 86, The Wildlife Society, 1984:66 pp., 1 black-and-white photograph, 31 tables, 26 numbered text figs. $4.05.—The Wildlife Monograph series is designed to accommodate papers that are too long for publication in typical journal format. These papers tend to be highly data-oriented with much of the raw data

presented in tabular form, and they often resemble theses or dissertations in style and format. This number in the Monograph series reads like the latter. It attempts to answer the basic questions of what types of dead trees are used by cavity-nesting birds, how are they used, and how we can "manage" for increased use. To these ends the monograph is quite successful, providing much detailed information about cavity users, both primary excavators and secondary users, and their habitats in an isolated portion of the Sierra Nevada Range. The monograph is data-dominated and should provide useful information for students of "snag management" and cavity-using species in general. The presentation of so many data makes the monograph also quite useful for instructional purposes in advanced ecological courses. My graduate-level Statistical Ecology class went through the monograph in an attempt to "verify" some of the analyses. Our results, however, did not always conform with the authors'. For example, the dendrogram (Fig. 19) of multivariate foraging niche overlaps could not have been produced from the data in Table 21, regardless of what was presented in the text. Overlap between the Pygmy Nuthatch (*Sitta pygmaea*) and Brown Creeper (*Certhia americana*) (the two most similar species in the dendrogram) is approximately 0.5 in the figure, but only 0.264 in the table (where the two most similar are the Pygmy Nuthatch and White-breasted Nuthatch [*S. carolinensis*] at 0.476). When we repeated the UPGMA cluster analysis of the Table 21 data, a totally different dendrogram was produced. With this in mind, care should be taken when interpretation of tabular data from this monograph is undertaken, especially as the figures are attractive and may be placed, unchecked, in textbooks.

It is also a bit unclear as to when the data were collected and how the years were treated. We know that nesting cavity data were collected in 1976–1978, but we don't know when foraging observations and density estimations were conducted. Therefore, we don't know if data were collected in all years and lumped, or if just a certain year or years were used. For example, Figs. 22–24 analyze the density data. Some plots, however, are averaged from 1975 and 1976, while others are from 1977 only. How can this be valid? Are not year effects possible? Careful examination of the figures, especially the first two, shows that the shape of the line is determined almost entirely by the brush plot point which were (by chance?) the only data from 1975–76.

A similar problem is encountered in Table 26, a comparison of bird use before and after snag removal. Again the after-data are densities averaged over two years, 1975–76. However, the before-data were taken from a study by D. L. Beaver in 1972. Therefore, the before- and after-data not only have been confounded with yearly differences but investigator effect as well. Moreover, we are left to assume that identical sampling procedures were used.

Notwithstanding the plethora of analytical discrepancies, the monograph is valuable and should be read by all people interested in snag ecology. The price of $4.05 is well worth the investment.—ROBERT C. WHITMORE.

THE ECOLOGICAL WEB (MORE ON THE DISTRIBUTION AND ABUNDANCE OF ANIMALS). By H. G. Andrewartha and L. C. Birch. Univ. Chicago Press, Chicago, Illinois 1984:506 pp., 7 black-and-white illus., numerous tables and figs. $35.00—The relative importance of different biotic and abiotic factors in determining the distribution and abundance of animals continues to receive considerable attention (e.g., The American Naturalist issue devoted entirely to the subject [Am. Nat., 122:583–705], the recent volume edited by Strong et al. [Ecological Communities: Conceptual Issues and the Evidence, Princeton Univ. Press, Princeton, New Jersey, 1984], the Symposium on Competition at the 1985 A.O.U. meeting in Tempe, Arizona). But perhaps the most intriguing recent attempt at addressing this thorny issue is Andrewartha and Birch's "The Ecological Web." Although it bears a resemblance to their earlier work (The Distribution and Abundance of Animals, Univ. Chicago Press,

Chicago, Illinois, 1954), the authors state in the Preface that they hope the "book will be accepted as a new contribution to population ecology—not merely a revision of our previous work." Indeed, the book does include much new material, and, although the entire text may not be essential reading for all animal ecologists, portions of it merit scrutiny.

The book is divided into three parts: "The theory of environment," "General theory of population ecology," and "Population ecology as it is practiced." Each section covers considerable ground. There is everything from a formal mathematical definition of the environment of an animal to a closing chapter entitled "The ecology of man." Approximately 5% of the more than 700 references are bird papers.

The first section of the book, "The theory of environment," is rather meaty reading. Considerable space is devoted to the use of a graphical representation of the factors influencing the survival and reproduction of animals (i.e., biotic and abiotic components in the organism's environment). The resultant dendrogram, or, as the authors propose to call it, "envirogram," traces pathways taken by environmental factors of importance to the focal animal. The focal animal's environment is conceptualized as including a "centrum" of directly acting components, comprised of mates, predators, resources, and malentities, surrounded by a "web" of indirectly acting components. According to Andrewartha and Birch, malentities are hazards that differ from predators in that the former's reaction to the focal animal is either negative or lacking rather than positive, as would be a predator's reaction. Resources include not only traditional components such as food, water, and heat, but also "tokens" such as daylength (i.e., signals that the focal animal uses to prepare for the future). Environmental components are viewed as being important only if they have the capacity to vary. Natural objects can constitute more than one component if they do different things to the focal animal (i.e., interact at different levels). Although this "theory of the environment," which is really a viewpoint from which to examine an animal's ecology, is a bit overwhelming at first (an entire lexicon is developed in the first 50 or so pages), adopting it should provide autecologists with a more holistic view of an organism's environment. Its use may actually allow "naturalists" to codify their multi-factored approach to ecological study. I especially liked the envirogram, which will allow researchers to illustrate graphically, albeit in telegraphic form, the current state of knowledge of the ecology of their animal. For this first section alone, the book is worth reading.

I found the remainder of the book considerably less useful. Much of what is discussed in Part 2 of the book has been covered as well or better before, some of it in the authors' earlier work. The literature is certainly not biased toward North American studies, as are so many of our own locally authored volumes on the subject; but I found numerous instances in the book where the presentation of material would have been strengthened had more North American sources been used. But then again, it is nice to read about what ecologists elsewhere are doing. Part 3 is an application of Parts 1 and 2 to the ecology of several animals, and includes a total of 30 pages on the Black-backed Magpie (*Gymnorhina tibicen*) and Grey Teal (*Anas gibberifrons*).

Because it shifts between the very detailed and the very general, I found the text difficult to read and unconvincing in places. Overall, however, a well-seasoned ecologist should be able to separate the wheat from the chaff. (Although I doubt that all will agree on which segments constitute the former and which are the latter.) The book is well suited for graduate students about to embark on thesis research. It should both encourage and humble these readers. Andrewartha and Birch conclude with the message that an animal's world, like our own, is a rather complex place, and that attempting to understand it requires more than simple models. Whether the book has any effect on the approach taken by autecologists in North America should be apparent by the presence or absence of "envirograms" in their future presentations and publications.—K.L.B.

UTAH BIRDS: A REVISED CHECKLIST. By William H. Behle, Ella D. Sorensen, and Clayton M. White. Occasional Publication No. 4, Utah Museum of Natural History, Univ. Utah, Salt Lake City, Utah, 1985:108 pp. $6.25 (paper).—Without doubt Bill Behle and Clay White are qualified to write a book summarizing Utah birds. They sit as the Deans of Utah Ornithology (although I would like to have seen Keith Dixon included as an author on this book) and their respective contributions to the field are widely known. Bill has spent over 50 years working with Utah birds and has published many important papers and monographs. His famous "Birds of the Pine Valley Mountain Region Southwestern Utah" (University of Biology Section 7:1–85, 1943) greatly influenced my early work on the Virgin River Valley avifauna. Clay White has spent many years collecting birds throughout the state, with much of his early work under the direction of Dr. Behle. Clay's stories of collecting in the Manti LaSal mountains are classic! (Imagine being trapped by high water and forced to live on the passerines you collected. Clay often said, "If you can't eat a bird don't shoot it.")

Therefore, I was pleased to see this checklist appear in print. It is a welcome addition to the two recent major works on the Utah avifauna (Behle, W. H. and M. L. Perry, Utah Birds, Utah Museum of Natural History, Salt Lake City, Utah, 1975; Hayward, C. L., C. Cottan, A. M. Woodbury, and H. H. Frost, Birds of Utah. Great Basin Naturalist Memoirs 1:1–229, Brigham Young Univ. Press, Provo, Utah, 1976). It is stated in the preface that the book was designed for field use and it easily fits in one's hip pocket.

This revised checklist summarizes recent records and brings the state's checklist into conformity with the "new" (1983) A.O.U. Check-list of North American Birds.

Included in the checklist are four basic lists: birds of unquestionable occurrence, those that "probably occur" or are "provisionals," "Unverified Species," and "Suspected Misidentifications." To make the first list the records are included only if there are two records which ". . . we judge to be acceptable . . . ." Provisionals ". . . have only one well-documented record which we judge to be acceptable." Unverified Species are ". . . based on sight records where supporting documentation is inadequate to demonstrate their unquestionable occurrence." The last group, "Suspected Misidentifications," is self explanatory. The authors have been most diligent in searching through the published records, and care is taken with each species to document the citations in the text. Moreover, the entire manuscript was reviewed by many noted Utah birders including the current authority on southwestern Utah birds, Jerome Gifford.

I have no major complaints with this work. The text is easy to read and well-documented. A random check of 30 text citations found all listed in the literature cited section. There are only a few typos, a credit to the University of Utah Printing Service. One might ask, however, why does the cover of a bird checklist have a leaf, a human skull, and what appears to be a chambered nautilus as the only illustrations? The lack of a detailed set of maps listing place names mentioned in the text detracts from the usefulness of the book as a field aid. I suggest that such maps be added to future editions. The inclusion of subspecies in the checklist seems a bit out of place as the 1983 A.O.U. Check-list does not list them. (Although it does support the subspecies concept.) Moreover, Behle's recent monograph, "Utah Birds: Geographic Distribution and Systematics" (Occasional Publication No. 5, Utah Museum of Natural History, Salt Lake City, 1985), gives an in-depth treatment (complete with maps) of the Utah subspecific avifauna. In sum, I recommend this fine work to anyone interested in Western birds. It is a valuable reference book.—ROBERT C. WHITMORE.

DISTRIBUTION OF OKLAHOMA BIRDS. By D. Scott Wood and Gary D. Schnell. Published for the Stovall Museum of Science and History, University of Oklahoma, Norman, Okla-

homa, by Univ. Oklahoma Press, 1984:xxi + 209 pp., 380 range maps. $14.95.—The recreational bird watcher in Oklahoma will find this book a valuable source of information in determining where and when to find the birds that occur in the state. The serious student of distribution and seasonal occurrences of Oklahoma birds will welcome the handy species summaries showing at a glance what is presently known and where gaps in information occur. After a short introductory section describing the purpose, format, and information used, the rest of the book consists of maps of Oklahoma showing, by use of circles in the county outlines, the counties in which a species has been recorded. There is one such diagram for each species that has been recorded five or more times in the state. Single letter abbreviations, carefully defined in the introduction, summarize the status and relative abundance of each bird. A bar graph shows seasonal occurrence. An appendix lists the species recorded in Oklahoma fewer than five times.

The symbols on maps showing county distributions signify whether there has been a collected specimen of the species or whether the county records are based on sightings alone. It would have been more informative if the symbols instead could have shown differences in seasonal distributions in the state. This approach, for example, would contrast breeding season and winter ranges in a permanent resident species that shows a shift between seasons, or would distinguish widespread transient individuals from summering distribution in a species that is both a migrant and nesting bird. But, the county marks only document presence regardless of season. The authors acknowledge this problem and explain that the records were not numerous enough in most cases to produce meaningful seasonal patterns.

It would seem that photographic records have the same confirmable reliability as specimen records, yet photographs are classed with sight records, maybe because both are obtained through a lens. There probably are also many sight records for a species in most of the counties where specimens were collected, and indeed a specimen constitutes a sight record before collecting. Recognizing these added sight records, it is obvious immediately from the maps how much more reliable sight records are in showing the total distribution of a species than are specimen records. Admittedly, there are errors in sight records that cannot be checked and this can produce some distortion (errors of commission), but these are minor compared to the greatly distorted reduction in range shown by the fewer specimen records (errors of omission).

There are two delightful line drawings in the book, both by Robert M. Mengel. They show the fore (frontispiece) and aft (cover) view of a Sprague's Pitpit (*Anthus spragueii*).—DOUGLAS JAMES.

BIRDS OF NEW YORK STATE. Including the 1976 supplement. By John Bull. Comstock Publ. Assoc., Division of Cornell Univ. Press, Ithaca, New York, 1974 (reissued 1985):xii + 703 pp., 82 black-and-white figs., 167 maps. $49.50 (cloth), $24.95 (paper).—That the Cornell University Press would reissue this book unchanged since 1976 attests both to the worth of the publication and to the presumed size of the potential market of New York bird watchers. The original edition was reviewed in the Wilson Bulletin (88:362–363 [1976]) and a somewhat more critical review appeared in the Auk (92:830–832). Little can be added to these reviews except to note that the color plates of the original are not in the reissue and the black and white photographs are poorly reproduced. The taxonomic innovations for which Bull was criticized in the earlier reviews are now seen to be advanced awareness of the changes made in the Sixth Edition of the A.O.U. Check-list, although of course the arrangement of species is still that of the Fifth Edition. The book has a definite historical value, but for accurate data on the present distribution and abundances of New York birds we await the publication of the Atlas of Breeding Birds now in preparation.—GEORGE A. HALL.

AFRICAN VERTEBRATES: SYSTEMATICS, PHYLOGENY, AND EVOLUTIONARY BIOLOGY. By Karl-L. Schuchmann (ed.). Proceedings of the International Symposium of African Vertebrates (1984), Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, West Germany, 1985:585 pp. with figs., line drawings, tables, photos, and color plates.—Twenty-seven of the 34 papers presented to the International Symposium on African Vertebrates in 1984 are published in the present volume, including 4 on mammals (pp. 11–90), 16 on birds (91–452), and 7 on reptiles and amphibians (pp. 453–585). All bird articles are in English except for one in French and 2 in German; the latter 3 have English summaries. All articles deal at least in part with evolution and systematics, with the following papers on specific groups: Fry, Keith, and Urban on ibises (*Bostrychia*), doves (*Aplopelia*), kingfishers (song phylogeny of *Halcyon*), and cuckoo host partitioning; Jensen and Stuart on the Cameroon mountain forest avifauna; Meyburg and Langrand on birds of prey (Falconiformes) of Madagascar; Crowe and Crowe on francolins (*Francolinus*); Tendeiro on guineafowl (Numididae) and their parasites; Short and Horne on barbets (Capitonidae); Schifter on mousebirds (Coliidae); Bock on the sugarbirds (*Promerops*); Farkas on the Madagascar Robin-Chat (*Copsychus albospecularis*); Sontag on the Wattled Starling (*Creatophora cinerea*); Louette and Herremans on bulbuls (*Hypsipetes*); Wolters on Afrotropical Estrildidae; and van den Elzen on African canaries and seedeaters (Carduelidae).

The remaining two papers (first two in the bird section) are comprehensive and extremely interesting as well as the most controversial of the presentations. Prigogine's paper (pp. 91–114) is a critical review of all new African species described or recognized from 1960 through 1983. In addition to detailed discussions of selected species, I found most useful his appendixes (especially Tables A.1 through A.3), which provide a list of new species recognized, with an assessment of present status and with all entries fully referenced. Certainly no one working on avian systematics of African birds can afford to overlook this paper.

The second comprehensive paper is by Sibley and Ahlquist (pp. 115–161) on the relationships of most suprageneric African groups based on data derived from the DNA–DNA hybridization technique. The summary (pp. 147–148) provides findings on 25 different groups; data, discussions, and phylograms of the various groups are provided in text and in the tables at the end of the paper. Of greatest interest to American ornithologists (in case you have not run into these conclusions in other Sibley-Ahlquist papers) are the following: flamingos (Phoenicopteridae) are members of the Ciconioidea and sister group of the ibis-shoebill-pelican-stork-New World vulture clade, with the storks and cathartines a sister group within that assemblage; the Coraciiformes include the trogons (suborder Trogones) as well as the rollers, kingfishers, and bee-eaters of the traditional Coracii; the Old World barbets (suborder Lybii) are a sister group to remaining "piciform" birds (suborder Pici) that include the New World barbet-toucan assemblage, honeyguides, and woodpeckers, but the order Piciformes is not the sister group to the Passeriformes; true shrikes (Laniidae) are a sister group of the Corvidae; larks (Alaudidae) are the sister group of other fringilloids; and the Ploceidae includes also wagtails and pipits (Motacillinae) and accentors (Prunellinae). Other startling findings in African groups include: divergence of flufftails (*Sarothrura*) from other Ralli at a level constituting a separate family and superfamily (Sarothruridae and Sarothruroidea); the Shoebill (*Balaeniceps*) is the sister group of pelicans; sandgrouse (infraorder Pterocletes with family Pteroclidae) are in the suborder Lari of the Charadriiformes; separation of the Bucerotiformes (hornbills and hoopoes) from the remaining Coraciiformes; the bush-shrikes (Malaconotinae) are a sister group of the Monarchinae within the Corvidae, and contain the tribes Malaconotini (most "bush-shrikes") and Prionopini, the latter not only including the "helmet-shrikes" but also vangids of Madagascar and the genera *Tephrodornis, Philentoma, Batis,* and *Platysteira*; African warblers (Cisticolidae) are distinct from other sylvioids and include the genera *Cisticola, Prinia, Hypergerus, Camaroptera,*

*Eminia, Apalis,* and probably other related ones; sugarbirds (Promeropinae) are part of the Nectariniidae, a finding in direct contrast to that in Bock's paper (pp. 349–374), which places this group in the Meliphagidae; and the Nectariniidae are the sister group of the Ploceidae. That these controversial findings "shake up" traditional views of avian relationships is unquestioned; yet it should be pointed out that, except for evolutionary branching points close enough to be within the range of experimental error in the technique and for the controversial matter of the time-scale conversion itself, I have not seen a definitive challenge to the Sibley-Ahlquist results. Systematists need to pay close attention to these data.

Overall, this volume is of great value (and probably indispensable) to avian systematists dealing with African birds.—BURT L. MONROE, JR.

COMMON BIRDS OF EGYPT. By Bertel Bruun, illustrated by Sherif Baha el Din. The American University in Cairo Press (distributed by Columbia Univ. Press, 562 West 113th Street, New York, New York 10025), 1985:50 pp., 14 color plates, in English and Arabic. $12.95 U.S.—This slim volume fills a long neglected gap in the ornithological literature of North Africa. It is unpretentious and does not claim to be anything but what it is, a very brief field guide to the most common birds of Egypt. It sets out to give the first-time visitor, tourist, or casual observer a handy guide to the birds one is most likely to encounter. This it achieves with some success. The illustrations, which are quite good, have suffered somewhat from an unfortunate choice of background colors that makes some of them hard to see.

The bilingual nature of the book should be useful in schools, etc., in Egypt and, perhaps, will create more interest and concern for the avifauna among the local people. One useful addition might have been an English transliteration of the local Arabic name for each species. I find the price a bit excessive.—ALAN HOLLETT.

BIRDS THAT CAME BACK. By John Gooders. André Deutsch Limited, London, England, 1983:xx + 178 pp., 8 color plates with captions, 46 black-and-white photographs with captions, 2 tables. $24.95.—The title of this book is somewhat of a misnomer in that the text covers not only British breeding birds that were extirpated on the island and subsequently returned, but also those that never recovered, those that never really disappeared, those that colonized Britain, and those that might do so. The book provides an overall history of birdlife in Britian, especially in relation to man's activities. It is concerned not only with birds that recovered due to conservation efforts, but also with species that have benefited from the results of human endeavors, including war. Especially interesting in this respect are the wetland species that gained a foothold due to strategic flooding of the coast during World War II, and the Black Redstart (*Phoenicurus ochruros*), which used the bombed-out buildings of London to become established in the 1940s. The intense ornithological interest of the British public has been both helpful to birdlife, in terms of an increased knowledge of species' distributions, and harmful, in terms of disturbance of rare breeders by hordes of anxious birdwatchers. The existence of a persistent band of egg collectors has been a particular hindrance to recovery attempts. Though the book provides interesting reading, it suffers from species accounts that are sometimes rambling and often repetitive, and from pictures that are not always located optimally with respect to the text. Gooders obviously writes to a British audience, which brings me to my main complaint. The book assumes a knowledge of the location of numerous British counties and towns. In a country roughly the size of Utah, a county is given the same status as a state or province in North America. The book's

geographic scale is much finer than this provincial North American can comprehend without some sort of reference. I would have benefited greatly from a map of Great Britain, complete with counties, major towns, and significant topographic features. In summary, this publication is probably not of general interest to those on this side of the Atlantic, but is better suited to those who are familiar with British birdlife and geography.—KEVIN M. DODGE.

MAGNIFICENT VOYAGERS. By Herman J. Viola and Carolyn Margolis (eds.). Smithsonian Institution Press, Washington, D.C., 1985:302 pp., many colored plates and black-and-white photos. $35.00 (cloth), $17.50 (paper).—The U.S. Exploring Expedition, 1838–1842 (often called "The Ex. Ex.") generally has been a little known event, but it represents the first attempt of the United States at a government-sponsored scientific expedtion. Under the command of Lieutenant Charles Wilkes, a small fleet of Navy vessels circumnavigated the world while making surveys of parts of South America, the Pacific Islands, the northwest coast of North America, and the Antarctic ice barrier (they were the first to identify land in Antarctica). Although it was largely a naval surveying expedition, a small group of scientists accompanied the Ex. Ex., collecting geological, botanical, zoological, and anthropological specimens.

To make this expedition more widely known, the Smithsonian Institution has assembled a special exhibition entitled "Magnificent Voyagers" and, in conjunction with the exhibition, has published this lavish volume about the Ex. Ex. Twelve chapters discuss the story of the expedition, various scientific collections, and survey methods. A brief biography of Wilkes is also included. There is also a chapter on the relationship between the Ex. Ex. and the Smithsonian, which ultimately (despite the reluctance of Joseph Henry, the first Secretary) became the repository of most of the collections. There are several useful appendixes, including a complete chronology of each ship during the four years. The Acknowledgment section details the history of the Smithsonian's exhibition (the "Ex. Ex. Ex."). Each chapter is profusely illustrated in both black-and-white and color with maps, contemporary woodcuts, and photographs of specimens. It is a coffee table book, but one that is packed with information.

Of most interest to W.O.S. members is the chapter by George E. Watson entitled "Vertebrate Collections: Lost Opportunities," the bulk of which is devoted to birds. The bird collections were largely made by Titian Peale, and he painted many of the illustrations. The Ex. Ex. brought back over 2100 bird specimens, mostly from the Pacific Islands. Peale attempted to report on this collection and describe the novelties, but was hampered by the restriction placed on him by Wilkes that the specimens remain in Washington, which at that time had no adequate library and no comparative collections. Peale described 129 species as new, but some of these had been described earlier and some were described by others before the Ex. Ex. report appeared. About one-third of Peale's names are valid today. In one interesting case Peale figured the Laysan Albatross (*Diomedea immutabilis*), which was not actually described for another 52 years. Both Peale and John Cassin (who collaborated on the final report) believed that this bird and the Black-footed Albatross (*D. nigripes*) were merely different age classes of *D. brachyura*. Most of the ornithological comment in the chapter is given in the legends (often extensive) of the 11 reproductions of Peale's paintings and one photograph of a specimen. Today the condition of this collection is "woeful," to quote Watson. Many of the skins, particularly type specimens, were mounted and placed on exhibition for some years. Others have been lost or sent to other institutions.

The great delay in publishing the results of the Ex. Ex. (the bird and mammal report did not appear until 1858 under the authorship of Cassin, who by then had available the fine

collections in the Academy of Natural Sciences, Philadelphia), the highly restricted availability of the report when it did appear, as well as the cavalier treatment of the collection itself, all combined to make the contribution of the Ex. Ex. much less than it might have been—the "Lost Opportunities" of Watson's title. Nevertheless the expedition was a noteworthy introduction for the young United States into the world of science. This book will give you an interesting and enjoyable summary of the Ex. Ex.—GEORGE A. HALL.

VERTEBRATE FLIGHT: A BIBLIOGRAPHY TO 1985. By Jeremy M. V. Rayner. Univ. Bristol Press, Bristol, England, 1985:182 pp. $9.75 (soft cover). (Order from the author at Dept. Zoology, Univ. Bristol, Bristol BS8 1UG, England.)—This useful and up-to-date bibliography, so obviously a labor of love, includes approximately 2500 entries. Over 800 of the entries are from 1975 onward, and at least 100 of these are from 1985 or are in press. There are also numerous historical references including works by Aristotle, Darwin, Muybridge, and Nopsca. Although the scope of the bibliography is rather wide (e.g., for some reason not apparent in the titles, there are references to "flight" trajectories in seeds and fruits) and coverage is somewhat patchy (especially for the less recent entries), Rayner provides most avian researchers more than enough reading for the short- or long-term. Entries range from the very general to the very specific. Flight is defined herein to include flying underwater, and there are references to the "porpoising of aquatic birds and mammals" as well as to flight in flying fish, amphibians, reptiles, and mammals. The overwhelming majority of the list, however, is devoted to birds.

A subject index of 10 major categories (Energetics, Evolution, Morphology and Anatomy, etc.) and over 100 sub-categories is included. There is also a taxonomic index that includes an ordinal breakdown for nonpasserines and a familial breakdown for passerines. Unfortunately, there is little cross indexing. Although a brief search through one of my own areas of interest (reversed sexual size dimorphism in raptors) was commendably thorough, the list is obviously selective, and it would have been nice to have an indication of the sources searched (i.e., journal titles and years, etc.).

The body of the text, which is printed in dot-matrix, is relatively easy on the eyes. At $9.75 the book is a bargain for anyone in need of information on avian flight.—K.L.B.

VOICES OF THE NEW WORLD THRUSHES. By John William Hardy and Theodore A. Parker III. ARA 10, ARA records, P.O. Box 1237, Gainesville, Florida 32604–0347, 1985:Monaural Tape Cassette and 22 pp. booklet. No price given.—Having produced collections of the vocalizations of nightbirds, wrens, vireos, and jays, Bill Hardy and his ARA Records now give us an excellent collection of the sounds of thrushes. Included on the cassette are 66 of the 68 species known to breed in the western hemisphere. The missing ones are *Entomodestes coracinus* and *Turdus reeveii,* which apparently have never been recorded. The selected recordings are all of good quality, but of course some of the rarely recorded species are represented by samples less brilliant than the commoner species. Some 46 persons contributed recordings and the task of assembling them was a heavy one. Most species are represented by at least two examples and many are represented by up to 10.

The songs of the members of the genus *Turdus,* from the Falkland Islands (*T. falcklandii*) to northern North America (*T. migratorius*), may sound very similar to most of us, but we will marvel over the fantastic examples of the Lawrence's Thrush (*T. lawrenceii*), probably the best avian mimic in the world, which include 78 different imitations, most of which can be identified.

The accompanying booklet discusses thrush songs in general and then gives detailed data on each recording, often accompanied by some pertinent taxonomic comments suggested to the authors by the similarities or differences in songs. This set of recordings should have something for everyone: the student of vocalizations; the taxonomist who must, in some cases, respond to some of the comments in the booklet; or the person, like myself, who wants to call up memories of the high forest in the Sierra Madre (*Myadestes obscurus*), the Montana Rockies (*Ixoreus naevius*), or merely the spruce-clad mountains of home (*Catharus guttatus*).—George A. Hall.

Rails of the World, A Compilation of New Information, 1975–1983 (Aves: Rallidae). By S. Dillon Ripley and Bruce M. Beehler. Smithsonian Contributions to Zoology, No. 417, Washington, D.C., 1985:28 pp., 2 black-and-white photographs.—Since the publication of Ripley's "Rails of the World" in 1977 much has been learned of members of this elusive and interesting family. This short publication attempts to compile this new information as well as make corrections of certain errors appearing in the original monograph. One new species, *Rallus okinawae,* and 4 new subspecies have been described since 1977. Besides these additions to the list, new information on taxonomy, undescribed plumages, ecology, behavior, nesting observations, and calls are given for other species. Status reports on certain endangered populations are summarized. A valuable supplement to the original monograph.—George A. Hall.

# ANNOUNCEMENTS

## CALL FOR ASSISTANCE

We seek male and female reproductive tracts, gonads, and cloacae from sexually mature birds of any species, except domestic poultry, for anatomical studies of the structures involved in phallic tumescence, ejaculation, and semen dilution. We plan to describe the gross anatomy, innervation, vascular supply and drainage, lymphatic system, and myology of the cloacal region in as many species as are made available. Our efforts are aimed at (1) increasing our basic understanding of the region, (2) assisting investigators who are developing and using artificial means of semen collection, and (3) verifying the presence or absence of oviductal sperm-storage tubules.

Please contact Murray R. Bakst, Avian Physiology Laboratory, Agricultural Research Service, USDA, Beltsville, Maryland 20705; or call (301)344-2545 for further information.

## HAWK MOUNTAIN RESEARCH AWARD

The Hawk Mountain Sanctuary Association is accepting applications for its 10th annual award for raptor research. To apply for the $750 award, students should submit a brief description of their research program (5 pages maximum), a curriculum vitae, and two letters of recommendation by 15 October 1986 to Stanley E. Senner, Executive Director, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529. The Association's board of directors will make a final decision early in 1987. Only students enrolled in a degree-granting institution are eligible; both undergraduate and graduate students may apply. The award will be granted on the basis of a project's potential to improve understanding of raptor biology and its ultimate relevance to the conservation of North American raptor populations.

## SECOND INTERNATIONAL SYMPOSIUM ON BREEDING BIRDS IN CAPTIVITY

The Second International Symposium on Breeding Birds in Captivity, honoring the late Jean Delacour, will be held at the Sheraton Premiere, Universal City, California, 11–15 February, 1987. For further information contact Symposium Coordinator, International Foundation for Conservation of Birds, 11300 Weddington Street, North Hollywood, California 91601, (818)980-9818.

## THIRD WORLD CONFERENCE ON BIRDS OF PREY

The Third World Conference on Birds of Prey, sponsored by the World Working Group on Birds of Prey (I.C.B.P.), will be held in Eilat, Israel, 22–27 March 1987. For further information contact Dr. Robin Chancellor, c/o British Museum (Natural History), Cromwell Road, London SW7, England.



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## The Wilson Bulletin

*Editor* Keith L. Bildstein
Department of Biology
Winthrop College
Rock Hill
South Carolina 29733

*Associate Editors* Michael W. Collopy
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P.O. Box 6045
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Morgantown, WV 26506

*Color Plate Editor* William A. Lunk
865 North Wagner
Road
Ann Arbor, MI 48103

*Index Editor* Kathy G. Beal
616 Xenia Avenue
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### Suggestions to Authors

See Wilson Bulletin, 98:335–336, 1985 for more detailed "Information for Authors."

Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Sixth Edition, 1983) insofar as scientific names of U.S., Canadian, Mexican, Central American, and West Indian birds are concerned. Abstracts of major papers should be brief but quotable. In both Major Papers and General Notes, where fewer than 5 papers are cited, the citations may be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (AIBS, 1983). Photographs for illustrations should have good contrast and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, P.O. Box 21618, Columbus, OH 43221.

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### Membership Inquiries

Membership inquiries should be sent to Dr. Richard Stiehl, Department of Biology, Southeast Missouri State Univ., Cape Girardeau, Missouri 63701.

## CONTENTS

A NEW SPECIES OF ANTWREN (FORMICARIIDAE: *HERPSILOCHMUS*) FROM PERU, WITH COMMENTS ON THE SYSTEMATICS OF OTHER MEMBERS OF THE GENUS
*Tristan J. Davis and John P. O'Neill* 337

NESTING SUCCESS AND PRODUCTIVITY OF HUMMINGBIRDS IN SOUTHWESTERN NEW MEXICO AND SOUTHEASTERN ARIZONA ..... *William H. Baltosser* 353

THE HISTORY OF THE SOUTHERN FLORIDA WOOD STORK POPULATION
*James A. Kushlan and Paula C. Frohring* 368

THE EVOLUTION OF REVERSED SEXUAL DIMORPHISM IN OWLS: AN EMPIRICAL ANALYSIS OF POSSIBLE SELECTIVE FACTORS ..... *Helmut C. Mueller* 387

WINTER POPULATION DYNAMICS OF THREE SPECIES OF MAST-EATING BIRDS IN THE EASTERN UNITED STATES ..... *Kimberly G. Smith* 407

SOCIAL ORGANIZATION, MOVEMENTS, AND HOME RANGES OF BLUE GROUSE IN FALL AND WINTER
*James E. Hines* 419

SUBSPECIES OF THE GREATER SCAUP AND THEIR NAMES ..... *Richard C. Banks* 433

FOOD CONSUMPTION AND GROWTH ENERGETICS OF NESTLING GOLDEN EAGLES
*Michael W. Collopy* 445

GENERAL NOTES

CLUTCH-SIZE DIFFERENCES IN WESTERN AND INTRODUCED EASTERN POPULATIONS OF HOUSE FINCHES: PATTERNS AND HYPOTHESES ..... *J. Timothy Wootton* 459

LATE FLEDGING DATES, RENESTING, AND LARGE CLUTCHES OF PRAIRIE FALCONS
*George T. Allen, Robert K. Murphy, Karen Steenhof, and Stephen W. Platt* 463

CHARACTERISTICS OF RED-SHOULDERED HAWK NESTS IN SOUTHEAST OHIO
*Mark S. Woodrey* 466

SPRIG DELIVERY BY BROAD-WINGED HAWKS
*David M. Lyons, Kimberly Titus, and James A. Mosher* 469

REVERSE MOUNTING IN THE AMERICAN KESTREL
*Reed Bowman and Elizabeth M. Curley* 472

INTRASPECIFIC BROOD PARASITISM IN THREE SPECIES OF PRAIRIE-BREEDING SHOREBIRDS
*Mark A. Colwell* 473

SUSPECTED INTRASPECIFIC EGG DUMPING IN THE WHITE IBIS (*EUDOCIMUS ALBUS*)
*Peter C. Frederick and Mark A. Shields* 476

A CASE OF BROOD MIXING BY COMMON LOONS
*Paul I. V. Strong, John A. Bissonette, and Richard Souza* 478

USE OF FENCEPOST CAVITIES BY NESTING EASTERN BLUEBIRDS IN SOUTHWESTERN VIRGINIA
*Thomas A. Pierson and Patrick F. Scanlon* 479

LITTLE BLUE HERONS NESTING AMONG CATTAILS
*Richard T. Hoppe and Robert A. Kennamer* 482

SWALLOWS TAKING INSECTS FROM POND SURFACES
*Robert R. Cohen and Mark L. Dymerski* 483

DRINKING BY NORTHERN BOBWHITES IN TEXAS ... *N. L. N. S. Prasad and Fred S. Guthery* 485

SEVERE AGGRESSION BETWEEN FEMALE BLACK-HEADED GROSBEAKS ..... *Geoffrey E. Hill* 486

AN ALBINO GREATER SHEARWATER: FEATHER ABRASION AND FLIGHT ENERGETICS
*David S. Lee and Gilbert S. Grant* 488

ORNITHOLOGICAL LITERATURE ..... 491

ANNOUNCEMENTS ..... 418, 504

# The Wilson Bulletin

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Pale-billed Sicklebill *(Epimachus bruijnii)*, male displaying.
Watercolor by James Coe.

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# OBSERVATIONS ON THE ECOLOGY AND BEHAVIOR OF THE PALE-BILLED SICKLEBILL

BRUCE M. BEEHLER AND CAROL H. BEEHLER[1]

ABSTRACT.—We studied the ecology and behavior of the Pale-billed Sicklebill (*Epimachus bruijnii*) in northwestern Papua New Guinea. Vocal adult males defended small foraging territories. Boundary disputes involved counter-singing, chases, and displays by one male to the other. Movements of a focal male averaged 2 km/day. A 7-day range of this male covered 15 ha. We recorded the species consuming 7 species of food plants from at least 5 botanical families. Insect-foraging included use of the decurved bill for probing knotholes. Diet and mating behavior appeared to conform to that of typical polygynous birds of paradise. Evidence is presented indicating that this species inhabits the Sepik drainage, southeast of where the bird had been recorded previously. *Received 24 Sept. 1985, accepted 1 May 1986.*

The Pale-billed Sicklebill (*Epimachus* [*Drepanornis*] *bruijnii*) is arguably the least known of the birds of paradise (Paradisaeidae), and until recently it has been known in life from only a few brief observations (Ripley 1964, Gilliard 1969, Diamond 1981, Whitney 1986, B. W. Finch, in litt.). Sometimes called the White-billed or Lowland Sickle-billed Bird of Paradise (Gilliard 1969, Diamond 1981), the species is poorly known for three reasons: (1) it has a small geographic range confined to a little-explored region, (2) it is wary, and (3) it spends much of each day in the canopy vegetation of the interior of tall rainforest. Of the 4 species of *Epimachus* sicklebills, the Pale-billed is the only lowland-dwelling form, and until very recently was believed to occur only in Irian Jaya—the Indonesian province of western New Guinea (Cooper and Forshaw 1977, see Diamond et al. 1977, Diamond 1981, Whitney 1986).

The Pale-billed Sicklebill is a member of a morphologically anomalous genus, one of whose member species exhibits an insectivorous diet in

[1] NHB Room 336, Smithsonian Institution, Washington, D.C. 20560.

combination with polygynous behavior. Here, we (1) present information on sexual organization, use of space, diet and foraging, and courtship display; and (2) compare this species' behavior with that of other members of this remarkable family.

## STUDY AREAS

Between 14 July and 10 August 1984 we studied the Pale-billed Sicklebill at 3 sites in the lowlands of the West Sepik Province, northwesternmost Papua New Guinea. From 14 to 29 July, we worked at an alluvial forest site (Puwani) on the west bank of the Puwani River, 6 km SSE of the Bewani Patrol Post, 45 km from the coast (3°1′S, 141°10′E, 195 m elevation). The site was a large, undisturbed tract of flat, tall rainforest, with large-boled trees and a very high (ca 40 m) canopy.

We also observed the sicklebill for short periods on 3 days between 30 July and 4 August along the road southeast of Vanimo High School, ca 7 km SE of Vanimo town. Following this, we made a forest camp on the track to Krisa village, at a point ca 8.5 km SE of Vanimo, in low limestone hills. At this site (2°47′S, 141°20′E, 210 m), we studied the sicklebill in forest that differed markedly from that at Puwani in being lower-statured, with an irregular canopy and smaller-boled trees. The topography was quite rough, and the entire region was heavily dissected by small streams.

## METHODS

In order to observe and monitor activities of sicklebills at the Puwani and Krisa sites, we cut and strung ca 5 km of survey lines through forest inhabited by sicklebills, using the methods described in Beehler and Pruett-Jones (1983). Each transect was marked by a colored plastic line. When a specific observation was made from a transect, the line at this point was tagged with masking tape and the tag numbered. In this fashion the movements and calling posts of individual sicklebills could be mapped accurately using the data from a final field survey of the transect and marker points.

At first we sought to locate individual sicklebills within walking range of the camps. We then cut transect lines around vocal and active males. After following an individual male for several days, it was possible to begin predicting his daily use of space, and efforts were made to study details of diet, foraging behavior, and male courtship habits. Attempts to net sicklebills failed.

Vocal playback experiments were conducted at Puwani to measure male response to an apparent male intruder. The songs of a male recorded from Vanimo by Bret Whitney were played from a remote speaker 2.5 m high in a sapling in the forest. Playbacks were conducted within earshot of an active and vocal male. Songs were played at intervals typical for the species. Playbacks were attempted at both edge and center of a male's home range.

Additional data were obtained from notes on stomach contents made by field collectors. These were solicited from museums known to hold collections of birds from western New Guinea. A review of papers discussing this species provided no data on diet (cf. Diamond 1981).

Nomenclature follows Diamond (1972) and Beehler and Finch (1985).

## RESULTS

*Habitat selection.*—In the lowlands of the West Sepik Province, the Pale-billed Sicklebill is sparsely distributed through nearly all forested

habitats. It was vocal and common along the road in selectively logged hilly lowland forest within a kilometer of the coast as well as in the coastal limestone hills to more than 200 m elevation at the Krisa camp. It occurred at a lower density in the flat Puwani basin that lies between the Bewani Mountains to the south and the coastal limestone hills to the north. No birds were observed in either coastal mangroves or regenerating second growth, although we spent only brief periods in these habitats. The Pale-billed Sicklebill appears to prefer old forest with at least some large canopy trees, but will occasionally use selectively logged forest and forest edge. We could detect no special habitat requirements. It appears to be a forest canopy-dweller like its congeners.

*Diet and foraging.*—We made 17 observations of foraging sicklebills. These are supplemented by two stomach samples from specimens in the Museum Zoologicum Bogoriense, Bogor, Indonesia. Twelve document fruit-eating, and 7 are of insect-foraging. Frugivory by this sicklebill includes at least 7 plant species from 5 families, and these include: *Cyrtostachys* sp. (Palmae), cf. *Syndapsis* sp. (Araceae), *Ficus* sp. (Moraceae), *Sloanea* cf. *forbesii* (Elaeocarpaceae), and an unidentified fruit of a red liana.

One sicklebill took at least one of the specialized, arillate and capsular species that can be classified as a "bird of paradise fruit"—the *Sloanea* (cf. Beehler 1983b). A single territorial male was observed visiting the same large *Sloanea* on 3 days at Puwani. On 25 July this male sat in the fruiting *Sloanea* for more than 30 min, during which time it regurgitated more than 33 small seeds from an unidentified plant (none was *Sloanea*).

An understory arecoid palm with large loads of small fruit (cf. *Cyrtostachys,* see Essig 1977) was a common food plant at the Krisa site. We observed the sicklebill clambering head down onto the lax, heavily laden rachillae of this palm to take fruits. The palm was one of the more common plants in the forest at Krisa (more than 10 plants/ha), and we observed it being visited by the Lesser Bird of Paradise (*Paradisaea minor*) and the Twelve-wired Bird of Paradise (*Seleucidis melanoleuca*).

Insect-foraging habits were similar to those recorded for the Buff-tailed Sicklebill (*Epimachus albertisi*; Beehler 1983a, unpubl. data). The species was cryptic and wary, and feeding observations were difficult to obtain. Seven observations of insectivory were of birds probing into knotholes and worm holes in dead wood, 3 were of birds searching dead leaves, and 2 were of birds searching vertical or sloping bark or limb surfaces. This sicklebill did not chisel or hammer with its beak, a method commonly employed by the shorter-billed paradisaeine genera such as *Lophorina, Ptiloris,* and *Paradisaea* (Beehler 1985).

*Mixed species flocks.*—In his single observation of a Pale-billed Sick-

lebill in northern Irian Jaya, Diamond (1981) noted that the female-plumaged bird was part of a mixed-species flock that included the Rufous Babbler (*Pomatostomus isidorei*) and Rusty Pitohui (*Pitohui ferrugineus*). We saw sicklebills in mixed flocks 5 times (Table 1). In these foraging aggregations it was not uncommon to find 4 species of birds of paradise moving through the understory together, searching for fruit and insects. At Puwani, the flocks we observed often lacked birds of paradise and were dominated by numbers of smaller flocking insectivores (cf. Bell 1967). At Krisa, the birds of paradise were more numerous, more gregarious, and they appeared to join together into foraging flocks each day in the late morning and late afternoon.

On 3 occasions it appeared that the repeated call of the male sicklebill stimulated flock coalescence at the Krisa site. The sicklebill would call from a point in the forest middle story for a number of minutes, and males of the Magnificent Riflebird (*Ptiloris magnificus*) and Twelve-wired Bird of Paradise could be heard to call from sites progressively closer to the sicklebill, until the birds were all moving together in a foraging flock. At Krisa we found plumed males of these 3 species foraging in the understory at the same cluster of ripe fruit. From repeated daily observations of these male birds of paradise together at Krisa, it appears that they formed a regular daily association. Flocks at Krisa were unusual for another reason. The main components of these flocks—adult male birds of paradise—spent much of their time foraging for fruit.

*Male movements and home range.*—At the Puwani site we mapped the movements of a single adult male during 7 days (Fig. 1). This was possible to do without either radio-telemetry or color-marking because of the nature of the male's activities and because of the absence of other adult males from the home range of the focal bird. At Puwani, ranges of singing males were widely spaced and nonoverlapping. Our focal male ("male A") moved sluggishly over his exclusive home range in tall alluvial forest. We were able to monitor his movements because he called with considerable frequency and regularity (see following sections). During our observation period (19–28 July), the male remained within a 15-ha patch of undisturbed forest. We never heard or saw another male-plumaged bird in this range. We did not encounter vocal neighboring males within 150 m of the edge of this "territory."

Male A traveled ca 2 km/day in his small home range (Fig. 1). Major foraging flights averaged ca 100 m (N = 118, range = 20–300 m), and the male spent an average of 14 min/perch site (N = 120, range = 1–46 min). He often remained more than 30 min in a single tree, singing periodically.

At the Krisa site we focused on intermale dispersion and male boundary maintenance. Sicklebills seemed in greater abundance at this latter camp,

and intermale distance appeared reduced. Our focal male at Krisa (male B) held a territory that included our campsite, and as a result he was always within easy earshot. A neighbor male (male C) inhabited an abutting territory ENE of that of male B. In the late afternoon on 3 days, these 2 males confronted each other at what perhaps was a territorial boundary. A summary of the encounter on 7 August is typical: Initially, while perched more than 50 m apart, the birds counter-called for 7 min. Male B made short flights through the middle story. Then male C entered the range of male B and came to perch on the same branch as B. One bird displayed to the other, and the latter departed. They met again in another tree and began a cycle of visits and departures in which the actors apparently reversed roles. Periodically, the vocal activity waxed and waned. After 68 min the encounter ended with the 2 males retreating from each other.

We conducted vocal playback experiments with male A at the Puwani site on 5 occasions over 3 days, and once with a male near Vanimo High School. In 2 instances at Puwani, male A came to the site of the playback, in a single instance male A called more frequently but did not approach, and on 2 instances male A became silent and gave no evidence of approach. The male at the second site responded vocally but did not approach.

*Male vocalizations.*—As with the other sicklebills, vocalizations are important to the behavioral repertoire of the male Pale-billed Sicklebill. On 4 clear mornings the first songs of male B were given between 06:31 and 06:36. Calling frequency was highest in the half-hour 06:30–07:00, when the male delivered, on average, 1.15 advertisement songs/min (N = 81). This rate continued slightly in excess of 1 call/min until after 08:00, when it dropped to 0.8/min. Between 09:00 and 15:30 h, the male sang between 2 and 10 songs/h. Later in the afternoon calling frequency rose to slightly less than that recorded in the early morning.

The advertisement song of the male Pale-billed Sicklebill is distinct from those of the other 3 species of *Epimachus.* It is a string of hoarse or hollow whistled notes, sometimes preceded or ended by one or several low musical gurgles or coughs, e.g., *wik-kew KWEER KWEER kwer? kor kor kor* (we recorded considerable variation within and between individuals). It is moderately high-pitched, carries a considerable distance, and is sometimes suggestive of certain vocalizations of the Lesser Bird of Paradise (Whitney 1986) or the western population of the Magnificent Riflebird (cf. Ripley 1964). The main body of this song is a series of 4–6 plaintive, musical notes that either rise or fall sharply in pitch. In some instances the first few notes are upslurred and the final few are downslurred. The main portion of the song is often appended with soft or gurgled notes, usually at a lower pitch.

TABLE 1

COMPOSITION OF MIXED FLOCKS THAT INCLUDED PALE-BILLED SICKLEBILL

| Species[a] | Puwani | | Krisa | | |
|---|---|---|---|---|---|
| | 25 July 10:30 h | 5 Aug. 12:10 h | 6 Aug. 09:15 h | 6 Aug. 15:45 h | 7 Aug. 15:00 h |
| Pale-billed Sicklebill (*Epimachus bruijnii*) | 1 ♂, 1 FP[b] | 1 ♂, 1 FP | 1 ♂ | 1 ♂ | 1 ♂ (B), 1 ♂ (C)[c] |
| Twelve-wired Bird of Paradise (*Seleucidis melanoleuca*) | 1 ♀, 1 FP ♂ | 1 ♂ | 1 ♂, 1 FP | 1 ♂, 1 FP | 1 ♂, 1 FP |
| Magnificent Riflebird (*Ptiloris magnificus*) | | 1 ♂, 1 FP | 1 ♂ | | 1 ♂ |
| Lesser Bird of Paradise (*Paradisaea minor*) | | 1 FP | | 1 FP | 1 FP |
| Jobi Manucode (*Manucodia jobiensis*) | 1 | | | 3 | |
| Spangled Drongo (*Dicrurus hottentottus*) | 1 | 1 | 1 | | |
| Rufous Babbler (*Pomatostomus isidorei*) | 4+ | | 3+ | | |
| Variable Pitohui (*Pitohui kirhocephalus*) | | 3+ | 4+ | | |
| Rusty Pitohui (*Pitohui ferrugineus*) | 5+ | | | | |
| King Bird of Paradise (*Cicinnurus regius*) | | | 1 FP | | |
| Golden Monarch (*Monarcha chrysomela*) | | 1 | | | |

TABLE 1
CONTINUED

| Species[a] | Puwani | Krisa | | | |
|---|---|---|---|---|---|
| | 25 July 10:30 h | 5 Aug. 12:10 h | 6 Aug. 09:15 h | 6 Aug. 15:45 h | 7 Aug. 15:00 h |
| Rufous-backed Fantail (*Rhipidura rufidorsa*) | | 1 | | | |
| Olive Flycatcher (*Microeca flavovirescens*) | | 1 | | | |
| White-eared Catbird (*Ailuroedus buccoides*) | | | 1 | | |

[a] English and scientific nomenclature follows Beehler and Finch (1985).
[b] FP = female-plumaged bird, undetermined as to sex, unless indicated.
[c] Two adult males appeared in the same flock at what apparently was a territorial boundary.

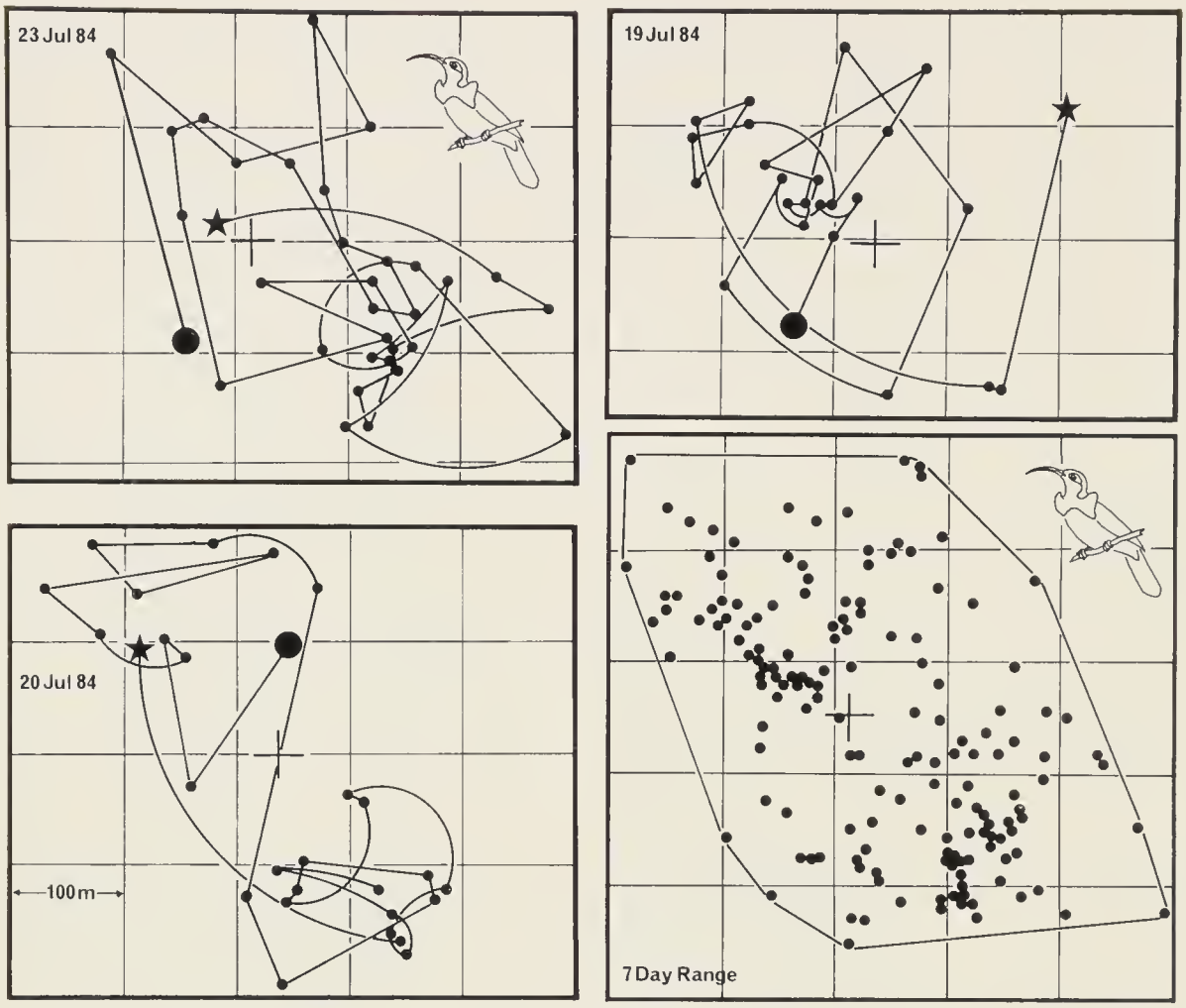


FIG. 1. Daily movements and 7-day home range of male A at Puwani. Three sample days of male movements are illustrated. The grid is 100 × 100 m. Large black circle indicates position of bird at beginning of day (not necessarily its roosting place).

Length of the advertisement song averaged 5.2 sec (N = 27, range = 3.7–7 sec); the median number of notes per call was 8 (N = 27, range = 5–10). The male sicklebill gave virtually no other call aside from this one. On occasion, while foraging, the male gave a quiet interrogative note, *whehn?*—very similar to those given by a number of the typical birds of paradise.

*Mating system.*—Unlike most avian families, the dominant mating system for the Paradisaeidae is polygynous court display (Beehler and Pruett-Jones 1983), and monogamous systems are known for only 4 of the 42 species. The Pale-billed Sicklebill exhibits none of the following characters exhibited by known monogamous birds of paradise: (1) paired foraging movements, (2) plumage monomorphism, (3) drab male coloration, or (4) active vocalization by the female. On the other hand, this sicklebill does show characters associated with polygynous birds of paradise: (1) considerable plumage dimorphism between the sexes, (2) male

erectile pectoral plumes, (3) elaborate posturing display by the male, (4) no significant vocalizations by the female, and (5) male foraging movements unassociated with females (Rand 1938, 1940; Beehler 1983c, 1985).

The Pale-billed Sicklebill has an activity pattern similar to that of the Buff-tailed Sicklebill as well as to that of the Superb Bird of Paradise (*Lophorina superba*) (Beehler and Pruett-Jones 1983). The male patrols his territory daily, displaying at different points and calling frequently, presumably to defend it from rival males, as well as to attract potential mates. Male-female bonding appears to be minimal, and it may be limited to mating. We have no information on nesting and nest care.

*Male display behavior.*—We did not observe full courtship or mating by the sicklebill. Once, at Krisa, we encountered a male displaying repeatedly in the cover of thick viny vegetation in the middle story of the forest interior. The male was attended by a female-plumaged individual, but we were unable to watch clearly either bird during the interaction that lasted several minutes. We encountered male display under 3 circumstances: (1) when the male was visited by a presumed female, (2) in the absence of conspecifics (a behavior common among other polygynous birds of paradise including the Buff-tailed Sicklebill) (Beehler 1983a), and (3) during male-male territorial encounters. In all 3 instances the male displayed in the lower middle story (ca 7–10 m) of the forest interior while perched on a small horizontal branch.

Display is preceded by delivery of the advertisement call, but the male gives no vocalizations while displaying. The high point of the display, however, is signaled by rapid rattling of the bill for a number of seconds.

On 5 occasions we observed a single stereotyped posturing display by the focal male (Frontispiece). The male perches upright on a branch, with his short upper pectoral plumes erected vertically, the longer, lower breast feather puffed outward into a wide skirt, and the tail fanned. The male holds this position with little movement (except for rattling bill) for as long as 10 sec. This upright posture is quite unlike the inverted display of the Buff-tailed Sicklebill, yet is quite similar to that of the Brown Sicklebill (*Epimachus meyeri*) (Crandall 1946).

*Female activities.*—Although the male is vocal and predictable, and hence conspicuous, the female appears practically nonexistent to the field worker. The female's unpreposessing plumage and silence make her nearly impossible to find without radio-tagging. This is also the case with the female Buff-tailed Sicklebill (Beehler, unpubl. data).

## DISCUSSION

In spite of its rather unusual appearance, in all other respects, the Pale-billed Sicklebill appears to be a typical bird of paradise. Our preliminary observations indicate the species has the type of court-based, polygynous

mating system that is known or strongly suspected for at least 34 of the birds of paradise (Beehler and Pruett-Jones 1983). Like most of the typical paradisaeid species, the Pale-billed Sicklebill has a diet that includes significant proportions of fruit and insects (see Schodde 1976, Beehler 1983b), and thus this bird differs from its presumed closest relative, the Buff-tailed Sicklebill, whose diet includes little fruit (Beehler 1983a, unpubl. data).

One characteristic of the genus *Epimachus* is the long decurved bill. At least two of the species (*albertisi* and *bruijnii*) use this bill for specialized knothole probing that is presently unknown in any other Papuan species.

Two species of sicklebill appear to be predominantly frugivorous (*bruijnii* and *fastuosus*), while the other pair (*meyeri* and *albertisi*) are predominantly insectivorous (Gilliard 1969, Schodde 1976, Beehler and Pruett-Jones 1983). The 2 frugivores exhibit bills that are measurably broader and less decurved than those of the 2 insectivores. The dichotomy does not follow present subgeneric lines; the 2 short-tailed sicklebills are presently placed in the subgenus *Drepanornis* (cf. Diamond 1972, Schodde 1976) while the 2 long-tailed species are considered true *Epimachus* (Gilliard 1969).

Whereas most birds of paradise are montane, the Pale-billed Sicklebill is lowland-dwelling. And, although other sicklebills show relatively large geographic distributions, the Pale-billed has a very small range, confined to the northern lowlands of western New Guinea (cf. Diamond 1981). In 1983 Bret Whitney recorded this species for the first time from Papua New Guinea. In his paper, Whitney (1986) supposed that the bird's range may be more extensive than previously recognized. In our field study we obtained indirect evidence that this sicklebill occurs in the vast Sepik drainage, to the south and east of where the bird has been recorded. Our chief field assistant, Simon Nako, knew the bird by its song and easily led us to the species when we first arrived in the area. He told us that he came to know the species while growing up at his village (Utai) in the western Sepik drainage, on the southern side of the Bewani Mountains. If the Pale-billed Sicklebill is widespread in the Sepik drainage, that it has been overlooked is not surprising. Unless one knows its voice, the bird is very difficult to observe. It has been overlooked by experienced naturalists who have spent considerable periods in the field where the bird occurs. If this sicklebill occurs, undetected, through large parts of the Sepik (New Guinea's third largest river system), one must consider that vast rainforest region in need of additional ornithological exploration.

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# POTENTIAL USE OF FEATHER CHEMISTRY AS AN INDICATOR OF RELATIVE GROWTH

GARY R. BORTOLOTTI[1] AND JON C. BARLOW[2]

ABSTRACT.—We explored the potential for using the elemental composition of feathers as an indicator of intraspecific variation in postnatal development. Instrumental neutron activation analysis (INAA) was used to determine the chemical profile of back and tail feathers of Bald Eagle (*Haliaeetus leucocephalus*) nestlings from Saskatchewan. Growth variables included parameters of Gompertz equations for weight, the rate of body feather development, the rate and timing of rectrix growth, and the age at which the nestlings made their first flight from the nest. There were significant correlation and multiple regression analyses involving growth parameters and the concentrations of sodium, chlorine, magnesium, manganese, calcium, and aluminum, but not bromine. Results often differed between the sexes and between the 2 types of feathers. Eaglets with rapid growth generally had higher concentrations of elements than birds with slower growth. Use of INAA may alleviate some of the problems associated with traditional means of collecting data on avian growth. *Received 29 July 1985, accepted 31 March 1986.*

Assessment of intraspecific variation in avian growth is frequently a laborious exercise requiring repeated visits to many nests to weigh and measure nestlings. A study of large nidicolous birds such as eagles (Accipitridae), for example, may require in excess of 100 days in the field. In addition, traditional means of data collection may not be suitable for all species. There are some birds, by virtue of their sensitivity to investigator-induced disturbance (e.g., Fetterolf 1983) or inaccessibility of nests (e.g., on sea cliffs), for which it is unwise or difficult to quantify postnatal development. When such difficulties prevail, a biochemical parameter that is easily measured and indicative of growth rate would be valuable.

In this paper we explore the possibility that the elemental composition of feathers can be used as an indicator of the relative growth of Bald Eagle (*Haliaeetus leucocephalus*) nestlings. Feather chemistry has been investigated as a means of identifying the geographic origins of migrating and wintering populations of birds (e.g., Hanson and Jones 1976, Parrish et al. 1983), and as an indicator of environmental pollution (e.g., Berg et al. 1966, Rose and Parker 1982). Several different analytical techniques have been used to determine the concentrations of various elements (e.g., Kelsall et al. 1975, Kelsall and Burton 1977, Rose and Parker 1982); we employed instrumental neutron activation analysis (INAA). By our meth-

[1] Faculty of Forestry, Univ. Toronto, Toronto, Ontario M5S 1A1, Canada.
[2] Dept. Ornithology, Royal Ontario Museum, Toronto, Ontario, M5S 2C1, Canada; and Dept. Zoology, Univ. Toronto, Toronto, Ontario M5S 1A1, Canada. (Author to whom reprint requests should be made.)

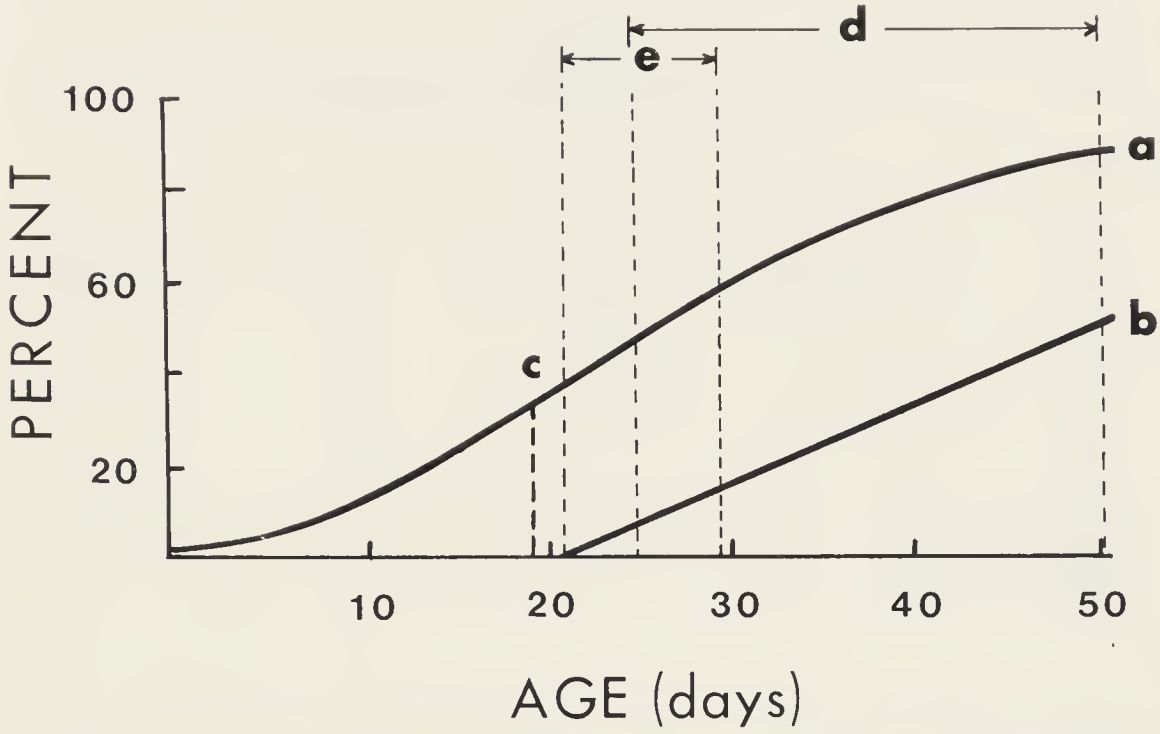


FIG. 1. Development of nestling Bald Eagles (sexes averaged) in relation to age prior to the time of feather collection (at about 50 days old): (a) weight growth as a percent of asymptotic size, (b) central rectrix growth as a percent of final size, (c) inflection point of the weight growth curve, (d) approximate time span from unsheathing to clipping of the back feathers (actual emergence from the skin is somewhat earlier), (e) approximate period of growth represented by the rectrix sample.

od, feathers are irradiated with neutrons from a nuclear reactor. These neutrons interact with the nuclei of the atoms in the feathers, and in doing so create radioisotopes. Gamma rays, with energies specific to each element, are emitted during the radioactive decay of the feather, and are measured by a spectrometer. Estimates of the concentrations of several elements are made simultaneously.

## MATERIALS AND METHODS

*Study subjects.*—Feathers of wild nestling Bald Eagles were collected at Besnard Lake, north-central Saskatchewan (55°20′N, 106°00′W). Nestlings were of known age, and sex was determined by size (Bortolotti 1984a). Back feathers were collected in 1980, 1981, and 1982 in mid-July when the chicks were between 45 and 55 days old ($\bar{x}$ = 50.3). The feathers, clipped at random from the upper-middle area of the back just above the skin, had unsheathed about 20 days earlier (Bortolotti 1984b) and were approximately 40 to 50 mm long. The distal 55 mm of one of the outer rectrices was also collected from each nestling in 1981 and 1982. Based on the rate of elongation of the central rectrix (Bortolotti 1984a), the sample represented about 7 or 8 days of growth (Fig. 1). Feathers were also available from 4 female and 2 male Bald Eagles (>2 years old) live-trapped on Besnard Lake between 1980 and 1982.

TABLE 1
CONCENTRATIONS OF ELEMENTS IN THE BACK AND TAIL FEATHERS OF NESTLING BALD EAGLES

| Element | Back[a] | | Tail[b] | |
|---|---|---|---|---|
| | $\bar{x}$ | SD | $\bar{x}$ | SD |
| Br | 59.8 | 15.49 | 27.8 | 9.48 |
| Mn | 7.67 | 4.085 | 70.6 | 38.03 |
| Al | 17.8 | 11.06 | 118 | 119.4 |
| Na | 535 | 284.7 | 640 | 242.9 |
| Cl | 4390 | 1465 | 2540 | 1167 |
| Mg | —[c] | — | 521 | 219.7 |
| Ca | —[c] | — | 2230 | 766 |

[a] N = 46.
[b] N = 31.
[c] Percent error too large for reliable estimates.

Males and females were analyzed separately because Bald Eagles are sexually dimorphic in size and several growth parameters (Bortolotti 1984b). Further details on the study area and aspects of the biology of this population of eagles are described in Gerrard et al. (1983) and Bortolotti (1984a, b).

*Sample preparation and irradiation technique.*—Feathers were cleaned by manual agitation in 50 ml of ether for 3 min. Each sample was air-dried and placed in a polyethylene irradiation vial that had been rinsed previously with distilled water and dried. All samples were washed and irradiated within 3 to 4 months of collection. Further details are given in Bortolotti and Barlow (1985).

The SLOWPOKE reactor at the University of Toronto was used for all irradiations. Feathers were irradiated by a neutron flux between $1 \times 10^{11}$ and $1 \times 10^{12}$ n/cm$^2$·sec for 5 min. After a delay period of 4 min following irradiation, the gamma rays were counted for 5 min using one spectrometer (Canberra GE[Li] detector; 8100 series, 4096 channel Canberra analyzer; teletype printer). The intensities of the gamma-ray peaks were determined by automatic analyzer integration of manually selected spectral regions. Using this methodology, we irradiated and spectrometrically analyzed 10 feathers/h.

*Detection and statistical analysis of elemental composition.*—Eleven elements were detected by the analytical procedure used: iodine (I), bromine (Br), magnesium (Mg), manganese (Mn), copper (Cu), sodium (Na), vanadium (V), aluminum (Al), chlorine (Cl), calcium (Ca), and sulfur (S). In each sample, the Mg concentration was reduced by 16% of the Al concentration to compensate for the fact that $^{27}$Mg is formed when $^{27}$Al is bombarded with fast neutrons (R. G. V. Hancock, pers. comm.).

The precision with which concentrations could be estimated was not equal among elements or for the same element between the 2 types of feathers (Bortolotti and Barlow 1985). Only those concentrations that could be determined with a high degree of precision (<10% error; Bortolotti and Barlow 1985) were statistically examined. Data were transformed where appropriate to satisfy assumptions of parametric statistical tests.

*Growth variables.*—Individual Gompertz growth equations (Ricklefs 1967) were fitted to weight data on 26 males and 20 females collected from 1980 to 1982 to determine the growth parameters $a$ (asymptotic size), $K$ (a constant proportional to the overall growth rate), and $t$ (age at which the inflection point of the curve occurs). In addition, linear

TABLE 2

CORRELATIONS BETWEEN CONCENTRATIONS OF ELEMENTS IN BACK FEATHERS AND GROWTH PARAMETERS OF NESTLING BALD EAGLES

| Growth parameter | Sex | N | Element | | | | |
|---|---|---|---|---|---|---|---|
| | | | Br | Mn | Na | Al | Cl |
| Asymptotic weight | M | 26 | 0.007[a] | −0.116 | 0.070 | −0.096 | −0.017 |
| (*a*) | F | 20 | −0.025 | 0.003 | −0.044 | −0.051 | 0.019 |
| Weight growth | M | 26 | 0.134 | 0.314 | 0.085 | −0.073 | 0.218 |
| rate (*K*) | F | 20 | −0.092 | 0.486[b] | −0.087 | 0.480[b] | −0.224 |
| Weight curve | M | 26 | −0.330 | −0.076 | −0.241 | 0.265 | −0.411[b] |
| inflection (*t*) | F | 20 | 0.111 | −0.057 | 0.021 | −0.066 | −0.006 |
| Fledging age | M | 25 | −0.387 | −0.105 | −0.438[b] | 0.427[b] | −0.489[b] |
| | F | 18 | −0.140 | −0.083 | −0.132 | 0.102 | −0.147 |

[a] Correlation coefficient (*r*).
[b] $P < 0.05$.

regressions of age on central rectrix length were done to establish the rate of rectrix growth (the slope of the line) and the age when the feather emerged from the body (the intercept) for each eaglet. Although it was not the central rectrix that was chemically analyzed, presumably its growth is representative of all the feathers of the tail. The age at which the birds first flew from the nest (fledged) was determined from daily visits to the nests. Fledging age is a good indicator of overall development (Bortolotti 1984b). Eaglets of similar age can be strikingly different in appearance because of different degrees of body feathering. Nestlings were classified as "early" developers if the age at which feathers unsheathed was less than or equal to 26 days for the humeral tract, 30 days for head and back feathers, and 43 days for tarsal feathers; otherwise they were referred to as "late" developers (Bortolotti 1984b). As not every measure of growth was available for every bird, sample sizes vary slightly.

## RESULTS

Elements whose concentrations were determined with a high degree of precision were Mn, Al, Cl, Br, and Na in back feathers; and Mn, Al, Cl, Br, Na, Ca, and Mg in tail feathers (Table 1).

There were statistically significant correlations between growth parameters and concentrations of elements in both back (Table 2) and tail (Table 3) feathers. Multiple linear regression models were used to see if the entire chemical profile of feathers could be used as a predictor of growth. When back and tail feathers were analyzed separately, fledging age of females could be predicted by the elemental composition of tail feathers ($F = 8.39$, df = 7,4, $R^2 = 0.936$, $P < 0.05$, with significant sources of variation being Mg, Mn, and Ca concentrations), and the fledging age of males could be predicted by the elemental composition of back feathers ($F = 3.61$, df = 5,19, $R^2 = 0.487$, $P < 0.02$, with significant sources of variation

TABLE 3

CORRELATIONS BETWEEN CONCENTRATIONS OF ELEMENTS IN TAIL FEATHERS AND GROWTH PARAMETERS OF NESTLING BALD EAGLES

| | | | Element | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Growth parameter | Sex | N | Br | Mg | Mn | Na | Al | Cl | Ca |
| Asymptotic weight | M | 17 | 0.480[a] | −0.355 | −0.360 | 0.552[b] | −0.190 | 0.605[c] | −0.673[c] |
| (*a*) | F | 14 | −0.015 | −0.140 | −0.128 | −0.036 | −0.252 | 0.012 | 0.027 |
| Weight growth | M | 17 | −0.189 | 0.343 | 0.442 | −0.225 | −0.181 | −0.343 | 0.166 |
| rate (*K*) | F | 14 | −0.289 | 0.612[b] | 0.625[b] | 0.535[b] | 0.421 | −0.144 | 0.471 |
| Weight curve | M | 17 | 0.248 | −0.356 | −0.407 | 0.188 | 0.118 | 0.425 | −0.210 |
| inflection (*t*) | F | 14 | −0.068 | −0.301 | −0.257 | −0.213 | −0.091 | −0.097 | −0.268 |
| Fledging age | M | 16 | 0.080 | −0.262 | −0.166 | −0.126 | 0.095 | 0.063 | −0.245 |
| | F | 12 | −0.191 | −0.329 | −0.451 | −0.258 | 0.271 | −0.255 | −0.461 |
| Age rectrix first | M | 14 | 0.513 | −0.582[b] | −0.546[b] | 0.322 | −0.059 | 0.624[b] | −0.497 |
| emerged | F | 12 | 0.379 | −0.716[c] | −0.768[c] | −0.541 | −0.398 | 0.092 | −0.709[c] |
| Rate of rectrix | M | 14 | 0.098 | 0.069 | −0.085 | −0.085 | −0.332 | −0.011 | 0.183 |
| growth | F | 12 | −0.568 | 0.420 | 0.511 | 0.240 | 0.373 | −0.342 | 0.208 |

[a] Correlation coefficient ($r$).
[b] $P < 0.05$.
[c] $P < 0.01$.

TABLE 4
RELATIVE MAGNITUDE OF CONCENTRATIONS OF ELEMENTS IN RELATION TO ATTRIBUTES OF GROWTH OF NESTLING BALD EAGLES

| Attribute | Relative magnitude of concentrations | |
|---|---|---|
| | High | Low |
| Large body size | Na, Cl | Ca |
| Fast weight growth | Mg, Mn, Na, Al | |
| Early rapid weight growth | Cl | |
| Early fledging | Na, Cl | Al |
| Early rectrix growth | Mn, Mg, Ca | Cl |
| Early body feather development | Mn, Mg | |

being Mn concentrations). When the concentrations of back and tail feathers were used together, models predicting the $a$ ($F = 82.60$, df = 10,2, $R^2 = 0.998$, $P < 0.02$, all variables contributing significantly) and $K$ ($F = 21.76$, df = 10,2, $R^2 = 0.991$, $P < 0.05$, with significant sources of variation being Na, Al, Cl, and Ca concentrations in tail feathers) parameters of the weight growth equations of females were statistically significant.

The difference in feather chemistry between birds with early and late plumage development was tested with an analysis of variance (ANOVA) using sex and relative development as factors. Early and late birds were significantly different in the concentration of Mn in tail ($F = 4.39$, df = 1,28, $P < 0.05$) and back ($F = 4.61$, df = 1,32, $P < 0.05$) feathers, and nearly so for Mg ($F = 3.76$, df = 1,28, $P = 0.06$) in tail feathers.

Because sibling competition influences nestling growth (Bortolotti 1984b; 1986a, b) we examined the chemical profile of first-hatched vs second-hatched young within each brood. There were no significant ($P > 0.05$) differences in ANOVAs examining the effect of hatching sequence on the concentrations of elements. Similarly, Sign tests (Siegel 1956) of the difference between siblings were nonsignificant.

Birds with attributes generally considered to be desirable and indicative of good growth, such as early weight and feather development, rapid weight gain, and large body size, had higher concentrations of most elements than did birds with poor growth (Table 4). Mn, Mg, and Cl were the most consistent correlates of good development.

## DISCUSSION

The elemental composition of feathers is presumably influenced by the intake and absorption of elements into the bird and by various physio-

logical processes. There also is evidence that at least some concentrations of elements may be altered by environmental factors external to the bird after the feathers have matured (Rose and Parker 1982, Edwards and Smith 1984). Adsorption of ions may involve bonding on an ion-exchange basis. Other data suggest that feather chemistry may be relatively stable (Hanson and Jones 1976, Parrish et al. 1983, Bortolotti and Barlow 1985). Although the concentrations of some elements of some feathers potentially may be altered (e.g., by heavy metal pollution; Rose and Parker 1982), such chemical instability may not preclude the use of the elemental analysis of feathers as a research tool. Individual chemical identities of birds, even once modified, may still be obvious (Edwards and Smith 1984). In addition, when correlative evidence is sought, as it was in this study, absolute concentrations of elements may be of secondary importance. It does not seem plausible that an external source of contamination could bias our results to create several spurious correlations between mineral concentrations and various independent growth variables, especially as all of our birds were sampled from one lake in a consistent manner.

Several lines of evidence suggest that the chemical profiles of feathers are associated with biological functions within the bird. Most elements we detected showed some statistically significant relationship with one or more measure of growth (Table 4). Br, the only element not demonstrated to have any such relationship, has not been conclusively shown to perform any essential function in animals (Linder 1985). In their study of seasonal fluctuations in mineral content of Alaskan moose (*Alces alces*) hair, Flynn and Franzmann (1974) and Franzmann et al. (1975) found that the peaks of element concentrations coincided with the peak of physical condition. In particular, Mn and Mg fluctuated greatly and appeared to be related to seasonal differences in nutrition (Flynn and Franzmann 1974). Mn and Mg concentrations in feathers were associated with the weight, rectrix, and body feather growth of eagles (Table 4). In one respect, it is surprising that there are consistent significant correlations for an element among growth variables because most measures of development used in this paper are independent of each other. There is no correlation between the rate of weight and feather development (Bortolotti 1984b), or between fledging age and weight growth rate (Bortolotti 1986a).

It is possible that the trends reported here are not particularly strong because our sample included only apparently healthy chicks that survived to fledge. We did not examine the feathers of obviously stressed nestlings. An indication that feather chemistry may be related to physical condition came from data on a Bald Eagle that was captured at Besnard Lake in 1982. This bird was missing all the phalanges on one tarsus; very likely

the result of being caught in a trap set for furbearers (Bortolotti, pers. obs.). It was emaciated and could not fly. The back feathers of this bird had the lowest concentrations of Mn, Al, and Ca, and its tail feathers had the lowest concentrations of Mg and Cl of any feathers of eagles (not nestlings) analyzed from Besnard Lake. Data on nestling feathers are consistent with this observation; attributes of good growth were positively associated with most elements (Table 4). Hanson and Jones (1968) reported that captive Canada Geese (*Branta canadensis*) on experimental rations had abnormally developed primary feathers with much lower concentrations of most minerals compared to wild geese; however, the elements examined were not specified.

Bortolotti and Barlow (1985) show that feathers are not just sinks for the excretion of mineral surpluses as had been proposed by Hanson and Jones (1976). Rather the chemical profile is controlled to some degree by properties of growing feathers. Minerals, however, could be incorporated into feathers in a variety of ways. Concentrations would be inversely related to growth rate if deposition was time-dependent, i.e., if elements were incorporated into the feather at a rate per unit time as the feather grew. If such were the case, birds with similar plasma concentrations of elements could differ in feather chemistry because of differences in feather growth rate. For a given length of feather (as used in this study), a larger amount of an element would be deposited in a slow-growing feather. Results in Table 3 relating the rate of elongation of the central rectrix to concentrations in tail feathers fail to support the hypothesis of time-dependent deposition. Therefore, perhaps qualitative differences in growth and physical condition correspond with quantitative differences in mineral composition of the plasma and consequently the feathers. Controlled experiments are needed to investigate properly any causal associations between developmental processes and the chemical profile of feathers.

One might expect that feather chemistry would only be indicative of events that occurred during the period of growth represented by the portion of feather sampled (Fig. 1). Correlation and multiple regression analyses, however, suggest that fledging age may be predicted by feather chemistry. Male and female Bald Eagles fledge at a mean age of 78 and 82 days, respectively (Bortolotti, 1986b), considerably after the feathers used in this study were grown. This suggests that fledging age may be influenced by factors operating during an early stage of development.

A comparison of the data for back and tail feathers shows that they differ in their relationships to growth parameters (Table 2 and 3). These differences might be expected because the two types of feathers differ chemically (Table 1; see Bortolotti and Barlow 1985), and in the degree

of variation among individual birds (Bortolotti and Barlow, unpubl. data). Similarly, there is also little uniformity between the correlations of growth parameters and concentrations for males and females except for the age at which the rectrices emerged. There is no a priori reason to expect the sexes to have the same relationship between feather chemistry and growth, as males and females differ markedly in development (Bortolotti 1984b).

Given the preliminary nature of our results, and what little is known about feather chemistry, we believe that the elemental analysis of feathers is currently more valuable as a research or management tool than as a means of studying avian physiology. INAA has many desirable attributes as an analytical technique. It is highly sensitive, and a multitude of elements in trace concentrations can be detected simultaneously (Kruger 1971). Unlike many other methods, little preparation of the sample is necessary; there is no need for wet digestions, ashing, etc. INAA is nondestructive so samples may be repeatedly irradiated if necessary to test laundering methods, assess precision, or just reexamine samples that are outliers and thus may be errors. The birds used in the study need not be sacrificed, nor even harmed, for small masses (e.g., 0.003 g; Bortolotti and Barlow 1985) can be used in INAA. It is unlikely that the flying ability of most species would be impaired by the clipping of a small portion of one feather.

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# TIMING AND LOCATION OF SPRING SPERM RELEASE IN NORTHERN THRUSHES

W. B. Quay[1]

Abstract.—Cloacal lavages were taken from 166 individuals, representing 4 species of North American thrushes (*Catharus fuscescens, C. ustulatus, C. minimus, Hylocichla mustelina*) at 3 sites during spring migration and the beginning of the breeding season. Sperm morphology was similar in the 3 species showing sperm, and in second-year (SY) and after-hatching-year (AHY) males. Cloacal sperm were not evident in Wood Thrushes and Veeries south of their nesting ranges, but were found in Swainson's Thrushes at sites 800 and 230 km south of their nesting range. Sperm numbers in the lavages were not correlated with time-of-day, size of cloacal protuberance, wing chord length, or age class. *Received 10 Oct. 1985, accepted 21 Mar. 1986.*

Five closely related American thrushes nest at higher northern latitudes: the Wood Thrush (*Hylocichla mustelina*), Veery (*Catharus fuscescens*), Hermit Thrush (*C. guttata*), Swainson's Thrush (*C. ustulatus*), and Gray-cheeked Thrush (*C. minimus*). Ecological associations and behavioral traits of these species have been studied and compared extensively (Wallace 1939; Bent 1949; Dilger 1956a, b, c, d; Annan 1962; Cochran et al. 1967; Hicks 1967; Noon 1981). Relatively few aspects, however, of their reproductive biology have been described (Weaver 1939; Dilger 1956a, e; Brackbill 1958; Annan 1963; Longcore and Jones 1969). Published information on thrush sperm is limited apparently to that of Retzius (1909), who reported on morphology in European taxa, and McFarlane (1963), who examined sperm from 3 genera and 7 species of turdids, but provided no further specifications or details.

This report presents comparative data on the timing and geographic locations of spring sperm release in Wood Thrushes, Veeries, Swainson's Thrushes, and Gray-cheeked Thrushes based upon cloacal lavages (Quay 1984) of 166 individuals taken at 3 sites. Important findings include: (1) Sperm are released by some male Swainson's Thrushes prior to arrival at, and south of, the geographic nesting range of the species. (2) There are probable species differences in the timing and geographic location of first sperm release. (3) Timing of sperm release varies from year to year, probably in relation to timing of spring migration and associated environmental and physiological factors.

[1] Bio-Research Laboratory, 2003 Ida St., Napa, California 94558.

## METHODS

*Study sites and times.*—Collection of data and cloacal lavage specimens was at 3 sites (Table 1) that differed by being considerably south, slightly south of the nesting range, or well within the nesting range of the species studied. All species were lavaged at each of the sites, but the nesting ranges of only 2 of the species (Wood Thrush at Foley and Long Point, Veery at Long Point) encompassed one or both of the more northern sites.

The first site was a residential yard at the northeast end of the city of Galveston, Galveston County, Texas (29°19′N, 94°48′W), 1.6 km NW of the Gulf of Mexico. Birds were mist netted there at least several days per week throughout most of 1982, but spring migrant thrushes occurred during a limited period (Table 1). The second site was a farm 5 km NNW of Foley, Lincoln County, Missouri (39°08′N, 90°46′W), on the west bluffs of the Mississippi River Valley. Here diverse habitats were sampled with mist nets during the springs of 1983, 1984, and 1985. The third site was the "Old Cut Banding Station" of Long Point Bird Observatory (LPBO), within the base of peninsular Long Point, Ontario (42°34′N, 80°25′W). The site is within a major stopover area for migrating passerines (McCracken et al. 1981).

*Species, sex, and age characterization.*—All of the 166 thrushes contributing to this study were handled and lavaged by me. Thrushes in hand were readily identified to species, but sexing and ageing were frequently uncertain. A relatively large cloacal protuberance was taken to be the most reliable male criterion, and a distinct brood (incubation) patch was the most distinctive female criterion. Swainson's Thrushes were sexed by wing chord (Sheppard and Klimkiewicz 1976), but in rare cases when this was contradicted by cloacal protuberance or brood patch, the latter criteria were given priority. Spotted or streaked wing coverts constituted the sole criterion of second-year (SY) birds (Veery, Swainson's and Gray-cheeked thrushes) (U.S.D.I. 1977), although absence of such marks was not taken as a reliable indicator of older (ASY, after-second-year) age or "adulthood" (Payne 1961). Feather wear contributed additionally as an age criterion (Bond 1963).

*Cloacal lavage specimens.*—Cloacal lavages were taken within an hour of capture and just prior to banding and release (cf. Quay 1984; 1985a, b). On most occasions 2 lavages were made from each bird, the first without avoidable tactile stimulation and the second immediately following 20 gentle finger strokes bilaterally in the cloacal-vent region. The purpose of this was to try to ascertain whether cloacal sperm numbers and characteristics would be different in artificially stimulated emissions. Disposable plastic pipette tips (Cat. No. OME 1-100, Orthomedics, Inc., P.O. Box 247, Riverside, Connecticut 06878), fitted with rubber medicine dropper bulbs, were used to wash in and out of the cloaca aliquots of distilled or deionized water (salt crystals from alternatively tried saline solutions obscured sperm counts and caused artifacts). Such lavage aliquots were deposited on a clean 1 × 3 inch glass slide in sufficient volume to fill an elliptical area 40 × 20 mm.

The following improvements or modifications in previously reported techniques (Quay 1984, 1985a, b) were employed: (1) Slides ("Superfrost®," precleaned microscope slides, 1 mm thick, Cat. No. 12-550-12, Fisher Scientific Co., 711 Forbes Ave., Pittsburgh, Pennsylvania 15219) had one end frosted on one side to accommodate pencil labeling. (2) An ellipse, 40 × 20 mm inside dimensions, was marked on each slide using a cut cardboard or plastic guide and a red water-resistant felt pen, to retain a standard lavage volume on the slide. (3) A small (2 to 3 μl) drop of concentrated formalin was placed at the center of the elliptical area of each slide just before the lavage was added, both to fix the sperm and other lavage contents and to minimize the occurrence of artifacts during changes in tonicity and during drying. (4) Lavage pipette aliquot volumes of water of about 1.2 to 1.5 ml were employed. Generally 3 of these were combined per slide to fill the premarked elliptical area

TABLE 1

SITES, DATES, AND SPERM CONTENTS OF CLOACAL LAVAGES

| Site and year | | | Dates (number with sperm/total number lavaged) | | | |
|---|---|---|---|---|---|---|
| | | | Wood Thrush | Veery | Swainson's Thrush | Gray-cheeked Thrush |
| Galveston, Texas | | 1982 | 27 Apr.–6 May (0/4) | 25 Apr.–5 May (0/8) | 22 Apr.–7 May (0/13) | 18–28 Apr. (0/12) |
| Foley, Missouri | | 1983 | 7 May (0/1) | | 1 May (0/2) | 2 May (0/1) |
| | | 1984 | 2–10 May (2/2) | 7–11 May (0/3) | 2–14 May (2/39) | 2–14 May (0/21) |
| | | 1985 | 6–15 May (4/4)[a] | 28 Apr. (0/1) | 25 Apr.–1 June (0/9) | 28 Apr.–11 May (0/4)[a] |
| Long Point, Ontario | | 1985 | 18 May (1/2) | 17–24 May (3/11)[a] | 17–24 May (6/27)[b] | 19–23 May (0/2) |
| Totals | | | | | | |
| Females | | | | 0/1 | 0/1 | |
| Males | SY[c] | | | | 3/5 | 0/1 |
| | AHY[d] | | 6/7 | 1/2 | 4/44 | 0/5 |
| Unknowns | SY[c] | | | 1/4 | 0/2 | |
| | AHY[d] | | 1/6 | 1/16 | 1/38 | 0/34 |
| All groups | | | 7/13 | 3/23 | 8/90 | 0/40 |

[a] Includes one within-period recapture (e.g., one bird represented twice).
[b] Includes two within-period recaptures.
[c] SY = bird in second calendar year (year following hatching).
[d] AHY = bird in an after-hatching year (age otherwise unknown).

(total volume = 4.0–4.5 ml). After lavage of each bird, the pipette tip used was discarded and its bulb removed and thoroughly rinsed. Ordinarily neither the lavage water nor the lavage itself entered the bulb; however, avoidance of cross-contamination of slides by sperm from other birds or lavages is essential. Therefore, extreme care was taken to keep the slides, both before and after lavages, away from potential spattering during pipetting and by the birds themselves. Lavage slides (specimens) were labeled immediately, air-dried, and stored in dust-proof plastic slide boxes.

*Quantitative methods.*—Evaluation of the sperm content of the nonstained and noncovered cloacal lavages was done with phase contrast microscopy. The sperm head, or remaining portion closest to the head, constituted the point upon which sperm counts were based. When there were <500 sperm/slide, all sperm in the lavage area were counted; when there were between 500 and 50,000 sperm/slide, sperm were counted within 100 microscope field areas (0.079692 $mm^2$/field) at arbitrary intervals across and down the lavage area in a grid pattern; when there were >50,000 sperm/slide, they were counted within 50 such fields at arbitrary intervals. Total sperm/slide thus were counted (<500) or estimated (>500); estimations used the formula: sperm counted $\times$ $\pi ab$/number of fields $\times$ 0.079692, where $a$ and $b$ are the semiaxes (usually 20 and 10 mm) of the elliptical lavage area on the slide.

## RESULTS AND DISCUSSION

Thrush sperm in dried cloacal lavages were easily recognized on the basis of size, morphology, and optical properties. Cloacal sperm of the 3 species that released sperm were remarkably similar, at least at the level of phase contrast light microscopy (Fig. 1).

*Wood Thrush.*—None of the spring Wood Thrushes netted and lavaged at Galveston showed cloacal sperm, even though this locality is only about 150 km S and SW of the nearest limits of the species' breeding range (Oberholser 1974) on the Texas mainland. At the 2 sites within the nesting range, large fractions of Wood Thrushes lavaged in May had cloacal sperm (Table 1). Numbers of sperm per first lavage slide ranged from $1.6 \times 10^3$ to $196.0 \times 10^3$ without clear evidence of correlations with time-of-day, relative development of the cloacal protuberance (CP), or wing chord (Table 2). In 4 of 7 of the Wood Thrushes that released sperm, the post-massage lavage gave more sperm than the first lavage; 3 of these were the birds that gave the smallest numbers in the first lavage (Table 2).

*Veery.*—At Galveston and Foley, both south of the Veery's nesting range, none of 12 Veeries showed sperm. At Long Point, within the southern limits of the nesting range, 3 out of 11 individuals lavaged had sperm. One of these was an SY bird (spotted wing coverts) (Tables 1 and 2).

*Swainson's Thrush.*—This was the only species that released sperm south of the limits of its nesting range. Although sperm release was absent at Galveston, it occurred in 2 birds at Foley and in 6 at Long Point (Table 1). The latter 2 sites are 800 and 230 km S, respectively, of the limits of the nesting ranges. Sperm release at Foley was seen only in 1984, possibly because of smaller sample sizes in 1983 and 1985. The difference also

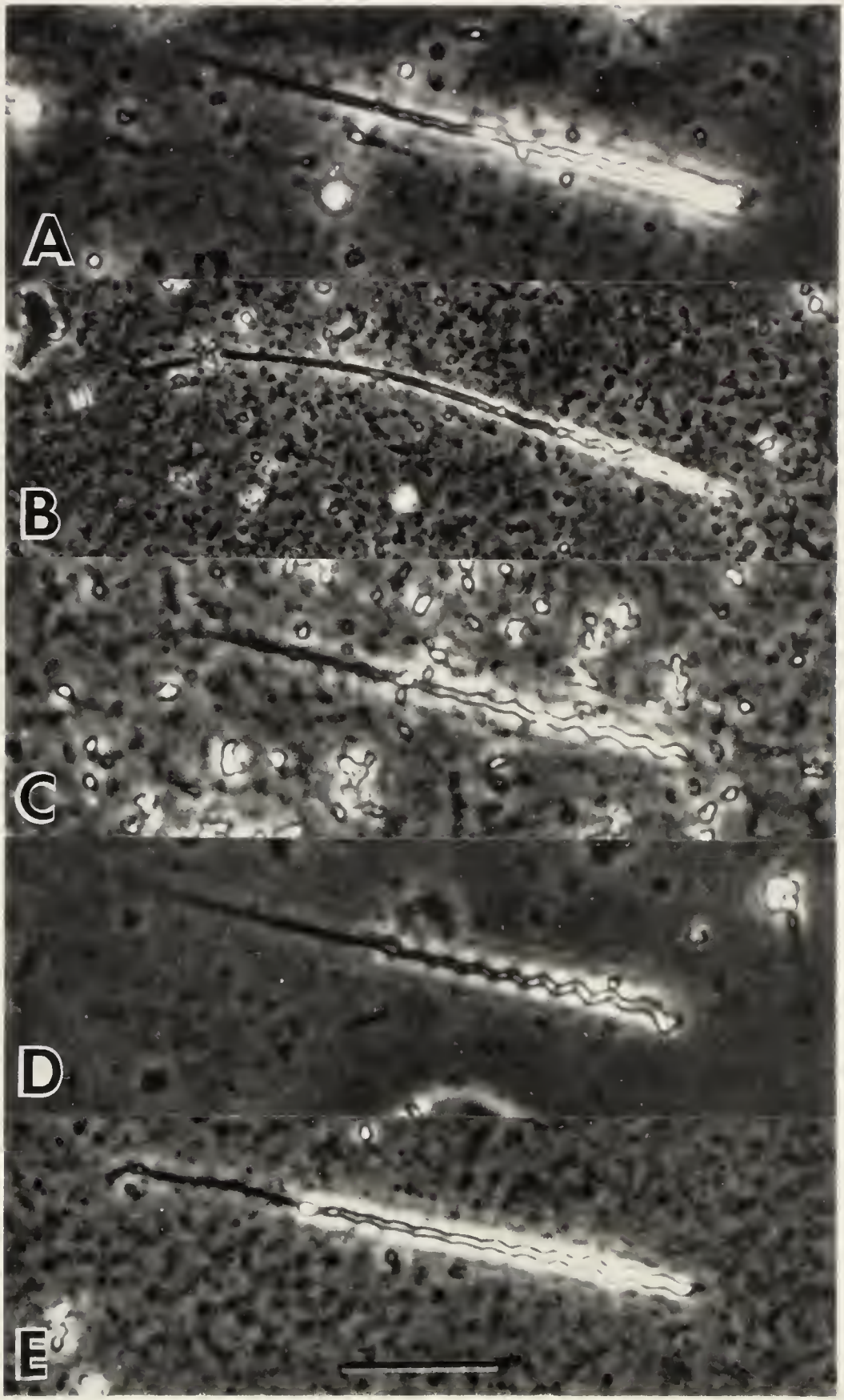


FIG. 1. Nonstained spermatozoa in cloacal lavages of thrushes, photographed with phase contrast microscopy. The relatively long, glistening, and spiraled heads are at the right, and

may have been influenced by the relatively early migration of Swainson's Thrushes in 1985, both at Foley and Long Point.

Maximum and mean cloacal sperm numbers were less in Swainson's than in Wood Thrushes (Table 2). This is more likely to be due to the representation of earlier phases of sperm release in the still migrating Swainson's Thrushes than in the largely on-territory Wood Thrushes, rather than to a true species difference in sperm numbers. Comprehensive quantitative cloacal sperm data from other free-living passerines have shown a characteristic increase in cloacal sperm numbers up to the third or peak phase of sperm release. This peak phase just precedes general occurrence of cloacal sperm in females (inseminated) of the particular population (Quay, unpubl. data). The present, more limited results from thrushes do indicate the efficacy and desirability of cloacal lavage samplings for comparing aspects of reproductive timing activity and potential in populations and species of thrushes. No relationships are evident between cloacal sperm numbers and time-of-day, relative size of the cloacal protuberance, wing chord length, or age (with vs without wing-covert spotting) for either species (Table 2).

*Gray-cheeked Thrush.*—None of the Gray-cheeked Thrushes lavaged at the 3 study sites had cloacal sperm (Table 1). As the distance between the most northern site and the southern limit of the nesting range of the Gray-cheeked Thrush is greater than the distance between the Swainson's Thrush's southernmost site with sperm release and its southern nesting limit, no conclusions can be drawn about possible differences between these species.

*Age differences.*—In Veeries and Swainson's Thrushes similar numbers of cloacal lavage sperm were released by SY and AHY birds (Table 2). Morphologically, as well as numerically, normal cloacal sperm were the same in the two age classes of birds (Fig. 1).

*Biological meaning of cloacal sperm.*—Results from cloacal lavages of free-living birds have indicated that reproductively active male passerines release sperm into the cloaca spontaneously and continuously (Quay 1984,

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the tapered, dark tails extend to the left. (A) Male Wood Thrush at 06:14 CST, 15 May 1985 (6th Wood Thrush from Foley in Table 2). (B) Male Veery at 12:36 EST, 24 May 1985 (3rd Veery from LPBO in Table 2). (C) SY (spotted wing coverts) Veery at 07:48 EST, 19 May 1985 (1st Veery from LPBO in Table 2). (D) Male Swainson's Thrush at 08:00 CST, 14 May 1984 (2nd Swainson's Thrush from Foley in Table 2). (E) SY (spotted wing coverts; absent to trace cloacal protuberance) Swainson's Thrush at 10:13 EST, 20 May 1985 (5th Swainson's Thrush from LPBO in Table 2). All at the same magnification; the bar scale is 20 $\mu$m long.

TABLE 2

NUMBER OF SPERM PER LAVAGE SLIDE AND OTHER CHARACTERISTICS OF THRUSHES RELEASING SPERM

| Species site | May date | Year | Time[a] | CP[b] | Wing chord (mm) | Wing covert spots[c] | Sperm per lavage slide | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | First slide | Postmassage |
| Wood Thrush | | | | | | | | |
| Foley | 2 | 84 | 08:00 | 1 | 107 | 0 | 1620 | 3630 |
| | 6[d] | 85 | 07:46 | 0–1 | 102 | 0 | 147,000 | 58,800 |
| | 7[d] | 85 | 17:50 | 2 | 102 | 0 | 196,000 | 12,200 |
| | 10 | 84 | 06:00 | 2 | — | 0 | 10,100 | 148,000 |
| | 15 | 85 | 06:14 | 4 | 105 | 0 | 8870 | 11,200 |
| | 15 | 85 | 07:48 | 4 | 106 | 0 | 92,400 | 21,900 |
| LPBO | 18 | 85 | 07:32 | — | 106 | 0 | 162,000 | 188,000 |
| Mean | | | | | | | $88.3 \times 10^3$ | $66.4 \times 10^3$ |
| Veery | | | | | | | | |
| LPBO | 19 | 85 | 07:48 | — | 95 | + | 28,100 | 17,500 |
| | 19 | 85 | 09:05 | — | 98 | 0 | 2190 | 1440 |
| | 24 | 85 | 12:36 | 1 | 102 | 0 | 35,300 | 37,800 |
| Mean | | | | | | | $21.9 \times 10^3$ | $18.9 \times 10^3$ |
| Swainson's Thrush | | | | | | | | |
| Foley | 12 | 84 | 06:00 | 0 | — | 0 | 0 | 493 |
| | 14 | 84 | 08:00 | 2 | — | 0 | 13,100 | 13,000 |
| LPBO | 19 | 85 | 09:07 | 1–2 | 96 | 0 | 8090 | 284 |
| | 19 | 85 | 09:59 | 4 | 99 | 0 | 5240 | 2040 |
| | 19 | 85 | 10:04 | 0–1 | 100 | + | 2 | 340 |
| | 20 | 85 | 09:56 | 2 | 99 | + | 64,300 | 18,000 |
| | 20 | 85 | 10:13 | 0–1 | 100 | + | 6620 | 20,100 |
| | 22[e] | 85 | 09:10 | 1 | 95 | 0 | 568 | 3500 |
| Mean | | | | | | | $12.2 \times 10^3$ | $7.2 \times 10^3$ |

[a] Central (Foley, Missouri) or Eastern (Long Point Bird Observatory, Ontario) standard time.
[b] CP = relative size of cloacal protuberance on a scale of 0 to 5.
[c] 0 = absent; + = present.
[d] The same bird; lavaged and banded 6 May, recaptured and lavaged 7 May.
[e] This bird was lavaged and banded 4 days earlier, at which time it was not releasing sperm.

1985a, b). This interpretation has been confirmed by recent studies with captive passerines lavaged at 3- or 6-h intervals (Quay, unpubl. data). As a number of nonpasserine groups of birds do not show this behavior, it can be concluded that spontaneous and continuous sperm release need not indicate proximate copulatory or ejaculatory activity. This is consistent with the finding in the present study that migratory and nonpaired (by field study) male Veeries and Swainson's Thrushes were releasing sperm relatively early, in relation to the well known trend of the later

arrival of females of the same species (Weaver 1939, Dilger 1956a, Annan 1962, Bond 1963). The possible competitive and adaptive advantages of early sperm release by male thrushes remain to be determined. Nevertheless, my data from a number of different passerines indicate that early sperm release per se may not be immediately or directly important for fertile inseminations. Its importance appears to be in appropriately timed build up and maturation of seminal emission and contents, leading to the most propitious timing, numbers, and characteristics of seminal sperm for effective mating.

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## COLOR PLATE

The Frontispiece painting has been made possible by an endowment established by George Miksch Sutton. The painting is by James Coe.

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# GROWTH OF NESTLING SAGE SPARROWS AND BREWER'S SPARROWS

KENNETH L. PETERSEN, LOUIS B. BEST, AND BRIAN M. WINTER[1]

ABSTRACT.—From 1980–1984, we characterized Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*) nestling growth and evaluated proximate factors potentially influencing growth in a southeastern Idaho shrubsteppe community. Increase in mass and tarsus length of both species was best explained by a logistic equation. For Sage Sparrows, all growth parameters we estimated varied significantly among years; 1983 seemed especially favorable for growth. Sage Sparrow mass growth rate and tarsus length at age 8 days declined significantly later in the breeding season, and tarsus growth rate varied inversely with brood size. In general, daily maximum temperature was negatively correlated with Sage Sparrow growth; weather seemed to have more effect early in the nestling period than later. Infestations of flesh fly larvae (Sarcophagidae) on Sage Sparrow nestlings were associated with reduced tarsus length near fledging. Little variation in Brewer's Sparrow nestling growth was explained by the variables we measured. Mass growth rate varied significantly among years and throughout the breeding season. Mass attained by age 7 days was greater in larger broods, but this effect was confounded by interactions among brood size, year, and seasonal effects. *Received 6 Dec. 1985, accepted 7 Apr. 1986.*

The diversity in growth patterns among birds is well documented (Ricklefs 1968). The pattern and rate of growth of a particular species ultimately may be determined by such factors as food availability (Lack 1968), predation pressure (Ricklefs 1984), or physiological considerations (Ricklefs 1979). Variation in rate and magnitude of growth within a species may be considerable (Zach and Mayoh 1982), and, although some of it likely reflects genetic variability within the species (e.g., Smith and Dhondt 1980), much of it may be attributed to the effects of extrinsic factors. For example, brood size (Best 1977, Bryant 1978), year (Ricklefs and Peters 1979, Price 1985), season (Best 1977, Ross 1980), habitat (Ross 1980, Rogers 1985), weather (Bryant 1975, Murphy 1985), and ectoparasites (Winterstein and Raitt 1983, Arendt 1985a) can influence nestling growth.

The Sage Sparrow (*Amphispiza belli*) and Brewer's Sparrow (*Spizella breweri*) are common species breeding in the Great Basin of the western United States (Wiens and Rotenberry 1981). Although considerable recent research effort has focused on the breeding ecology of these species (e.g., Wiens and Rotenberry 1979, 1981; Petersen and Best 1985), there is no published information on nestling growth. Documenting growth is desir-

[1] Dept. Animal Ecology, Iowa State Univ., Ames, Iowa 50011. (Present address KLP: Dept. Biology, Monmouth College, Monmouth, Illinois 61462. Present address BMW: The Nature Conservancy, 328 East Hennepin, Minneapolis, Minnesota 55414.)

able because it is potentially influenced by a variety of factors and thus may yield insight into other facets of the breeding ecology of these species. For example, growth rates might be used as indicators of territory quality or of stress resulting from environmental perturbation (Fendley and Brisbin 1977).

Our objectives were to (1) describe growth of nestling Sage and Brewer's sparrows and (2) evaluate the effects of year, season, brood size, weather, and ectoparasites on growth rate and magnitude. Few investigators have studied growth of a species for more than 3 breeding seasons. Our 5-year study contributes to our understanding of long-term variation in growth and provides a reliable data base from which to evaluate factors affecting nestling growth.

## STUDY AREA AND METHODS

Our study area was on the Idaho National Engineering Laboratory (INEL) site, 11 km south of Howe, Butte County, Idaho. The INEL site comprises sagebrush (*Artemisia* spp.) shrubsteppe habitat at an elevation of about 1500 m on the upper Snake River plain. Average annual precipitation is about 20 cm (Anderson and Holte 1981). Major shrub species were big sagebrush (*A. tridentata*) and green rabbitbrush (*Chrysothamnus viscidiflorus*); dominant grasses included bluebunch wheatgrass (*Agropyron spicatum*) and Indian rice grass (*Oryzopsis hymenoides*). Forbs were sparse, and much of the ground was bare.

Data were collected in the breeding seasons of 1980–1984. We initially established four 6.25-ha plots 200 m apart from each other, and additional data were collected in 1982–1983 from a 12-ha plot 1 km away. The latter plot had vegetation composition nearly identical to that on the 6.25-ha plots. Two of the 6.25-ha plots were partly burned in September 1981, and the 12-ha plot was partly burned in September 1982. In 1982, Sage Sparrow mass growth data from two of the 6.25-ha plots differed slightly but significantly from those of the other three plots, but in other years growth did not vary among plots. Thus, we pooled data across plots.

All plots were searched systematically for nests using a rope-drag technique (Petersen and Best 1985) that flushed attending adults from their nests. Many nests also were discovered incidental to our other field activities. Active nests were visited at 1- or 2-day intervals. During visits after hatching, each nestling's mass was measured to 0.1 g with a Pesola scale; left tarsus length was measured to 0.01 cm with calipers. Nestlings discovered within 4–5 days after hatching were aged by reference to the sample of known-age nestlings and were included in mean growth curves (Fig. 1). However, they were not used to calculate growth rates of individual broods and were excluded from all statistical tests.

Daily weather information, measured at Howe, was obtained from the National Climatic Center, Asheville, North Carolina. For each brood, we calculated mean daily maximum temperature and total precipitation for the entire period over which we measured the nestlings of that brood, and also for the first and second halves of the nestling period (0–4 and >4 days of age for Sage Sparrows, 0–3 and >3 days for Brewer's Sparrows). Each year, we calculated mean daily maximum temperature and total precipitation for the brood-rearing portion of the breeding season (approximately June–July) and also for the 2-month period (approximately April–May) preceding the appearance of most nestlings.

Most investigators who have modeled passerine growth have done so by using a logistic model. Accordingly, we described Sage and Brewer's sparrow growth with the logistic equa-

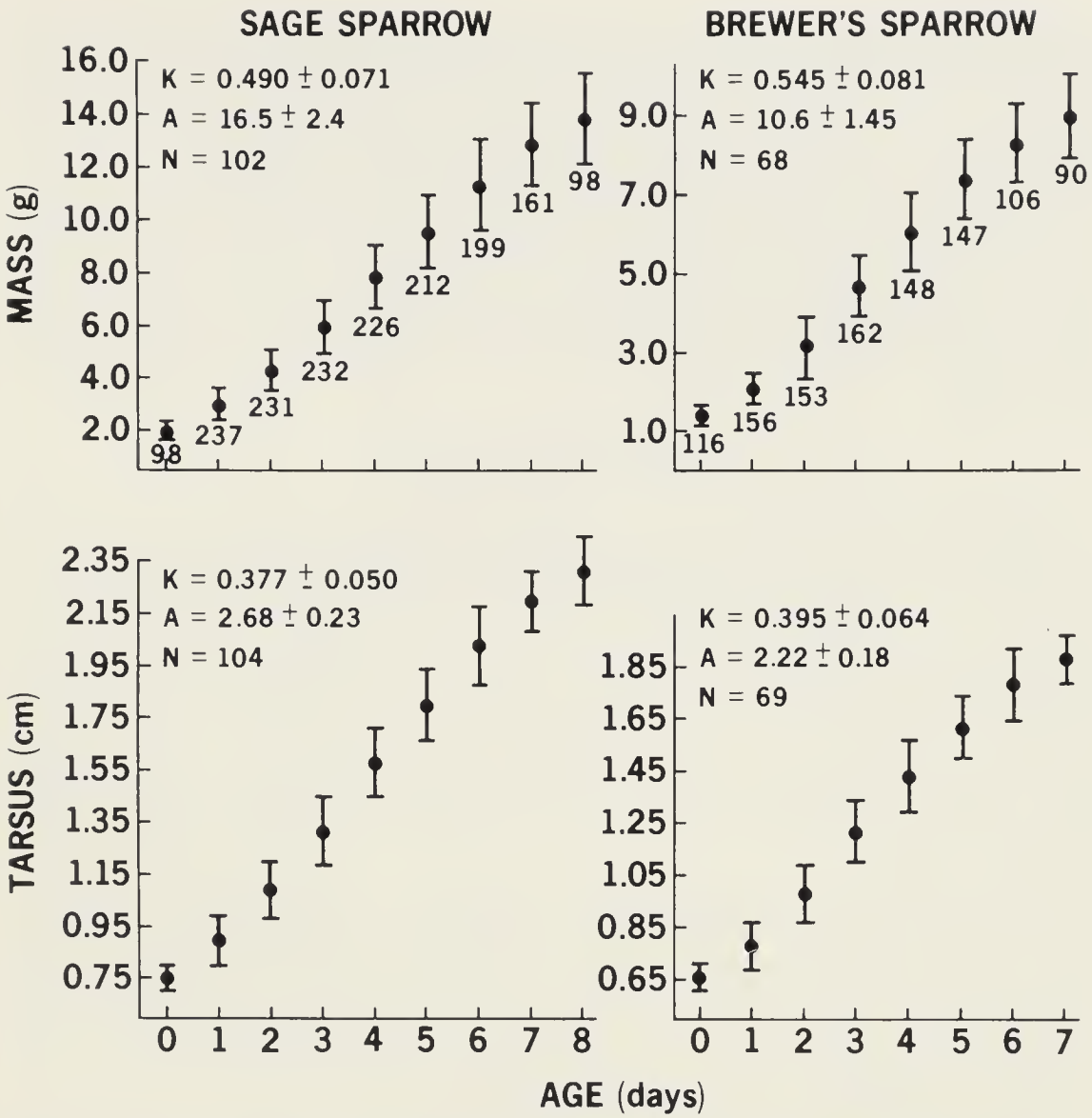


FIG. 1. Sage and Brewer's sparrow growth curves for mass and tarsus length. Dots and vertical bars represent $\bar{x} \pm$ SD; values below the bars are numbers of nestlings measured. K = growth rate constant (days$^{-1}$), A = asymptote (g or cm), and N = number of broods sampled.

tion, $Y(t) = A/\{1 + \exp[-K(t - I)]\}$, where Y(t) is the mass or tarsus length at age t days, A is the asymptote of the growth curve, K is a constant (days$^{-1}$) describing the rate at which the asymptote is achieved, and I is the age at the inflection point of the growth curve. Curve asymptotes were estimated, and curves were fitted to data by Ricklefs' (1967) graphical procedure. As Ricklefs recommended, we often adjusted asymptotes several times to obtain best-fit curves. As a further justification for our selecting the logistic model rather than a linear model to evaluate growth, we calculated coefficients of determination ($r^2$) for the mean growth curves (Fig. 1), using both models. Coefficients for the logistic model ranged from 0.997 to 0.999; those for the linear model were always less. We evaluated magnitude of growth by using measurements taken at age 7 (Brewer's Sparrow) or 8 (Sage Sparrow) days. (Brewer's Sparrows normally fledged at 8–9 days, Sage Sparrows at 9–10 days.)

For all statistical tests, broods, rather than individual nestlings, were used as sample units because measurements of nestlings within a brood were not independent. Three-way analysis of variance was used to examine variation in growth rate and in magnitude of growth among years, semimonthly periods of the breeding season (1–15 June, 16–30 June, etc.; each brood was assigned to a period based on hatching date), and brood sizes. Broods incurring partial loss of nestlings during the nestling period were not considered in analysis of brood size. *t*-tests were used to compare growth between broods with (>½ of the nestlings parasitized) and without (0 nestlings parasitized) infestations of flesh fly larvae. In none of our analyses were variances significantly heterogeneous. We used partial correlation analysis, with the effects of brood size statistically held constant, to evaluate relationships between growth parameters and weather variables. Unless stated otherwise, statistical significance was set at $P \leq 0.05$.

## RESULTS AND DISCUSSION

*General growth information.*—Changes in mass and tarsus length (Fig. 1) followed the sigmoid pattern common to many other passerines (Ricklefs 1968). On the day of hatching (age 0), measurements were relatively constant among nestlings of each species, but variation increased steadily as nestlings aged. Growth curves only began to level off about 1 day before fledging. Thus, growth was incomplete at fledging (see also, Austin and Ricklefs 1977, Rogers 1985). This could be an adaptation to decrease the time exposed to predators while in the nest, thereby enhancing survival (Ricklefs 1969).

Mean growth rate constants for mass (Fig. 1) were similar to those of other similar-sized emberizids (e.g., Ricklefs 1968, Maher 1973, Best 1977). Tarsus length increased at a substantially slower rate than mass; the mean tarsus growth rate constant for Brewer's Sparrows was considerably less than that reported by Best (1977) for the Field Sparrow (*S. pusilla*), a congener of the Brewer's Sparrow.

Ricklefs (1968) noted that R-values (ratio of asymptote to adult size) for mass were usually less than 1 for ground- and foliage-foraging species but often greater than 1 for aerial foragers. Because of the necessity for flight, aerial foragers must be well developed at fledging. Neither Sage Sparrows nor Brewer's Sparrows forage aerially (Winter 1984), and their R-values for mass were 0.85 and 0.97, respectively. (Adult sizes were obtained from mist-netted birds [Petersen 1982]; SS: mass = 19.3 ± 1.2 g [SD], tarsus length = 2.54 ± 0.08 cm, N = 166; BS: mass = 10.9 ± 0.7 g, tarsus length = 2.04 ± 0.05 cm, N = 83.) In general, Brewer's Sparrows fly more often during forays than do Sage Sparrows (Winter 1984), and this may account for the difference in R-values. Interestingly, R-values for tarsus length were greater than 1 for both species (SS: 1.06, BS: 1.09), suggesting the importance of early development of pedal locomotion.

*Annual variation.*—Growth rate and magnitude varied significantly among years for Sage Sparrows (Table 1). From 1980 to 1981, mass growth

TABLE 1

RESULTS OF 3-WAY ANALYSES OF VARIANCE OF NESTLING SAGE AND BREWER'S SPARROW GROWTH RATE CONSTANTS (K), AND MASS AND TARSUS LENGTH (TL) NEAR FLEDGING (AGES 8 AND 7 DAYS FOR THE TWO SPECIES, RESPECTIVELY) IN RELATION TO YEAR, PERIOD IN THE BREEDING SEASON, AND BROOD SIZE

| | Sage Sparrow | | | | | | Brewer's Sparrow | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Growth rate (K) | | | Measurements at age 8 days | | | Growth rate (K) | | | Measurements at age 7 days | | |
| | | *F* | | | *F* | | | *F* | | | *F* | |
| Source | df | Mass | TL | df | Mass | TL | df | Mass | TL | df | Mass | TL |
| Year | 4 | 2.50[a] | 5.01[a] | 4 | 5.76[a] | 8.10[a] | 4 | 2.73[a] | 1.30 | 4 | 1.68 | 1.25 |
| Semimonthly period[b] | 3 | 2.91[a] | 2.27 | 3 | 2.79 | 3.82[a] | 2 | 5.39[a] | 1.46 | 2 | 1.36 | 1.15 |
| Brood size | 3 | 0.24 | 4.42[a] | 3 | 0.39 | 1.38 | 2 | 1.63 | 1.76 | 2 | 15.45[a] | 0.04 |
| Year × period | 9 | 0.42 | 0.47 | 8 | 1.92 | 1.06 | 7 | 0.99 | 0.68 | 6 | 9.67[a] | 1.32 |
| Year × brood size | 12 | 0.61 | 0.88 | 8 | 0.84 | 0.88 | 7 | 1.05 | 0.66 | 3 | 9.36[a] | 0.22 |
| Period × brood size | 8 | 0.88 | 1.02 | 3 | 0.44 | 1.22 | 4 | 1.42 | 0.11 | 3 | 19.03[a] | 0.86 |
| Year × period × brood size | 5 | 0.91 | 2.17 | 0 | — | — | 4 | 0.42 | 0.49 | 1 | 31.87[a] | 1.27 |
| Residual | 54 | | | 20 | | | 35 | | | 17 | | |

[a] *F*-values are significant ($P \leq 0.05$).
[b] 1–15 June, 16–30 June, etc.; each brood was assigned to one period, based on hatching date.

TABLE 2

SAGE AND BREWER'S SPARROW NESTLING GROWTH PARAMETERS (MEAN ± SD) THAT VARIED SIGNIFICANTLY AMONG YEARS

| | Sage Sparrow | | | | | | Brewer's Sparrow | |
|---|---|---|---|---|---|---|---|---|
| | Growth rate (K) | | | Measurements at age 8 days | | | Growth rate (K) | |
| Year | N[a] | Mass | Tarsus length | N[a] | Mass (g) | Tarsus length (cm) | N[a] | Mass |
| 1980 | 17 | 0.484 ± 0.066 | 0.354 ± 0.045 | 12 | 14.4 ± 1.4 | 2.36 ± 0.08 | 16 | 0.577 ± 0.084 |
| 1981 | 20 | 0.459 ± 0.047 | 0.358 ± 0.027 | 9 | 13.6 ± 1.7 | 2.30 ± 0.09 | 13 | 0.509 ± 0.053 |
| 1982 | 22 | 0.497 ± 0.098 | 0.392 ± 0.060 | 16 | 12.6 ± 2.1 | 2.22 ± 0.15 | 11 | 0.579 ± 0.066 |
| 1983 | 29 | 0.517 ± 0.076 | 0.397 ± 0.054 | 18 | 14.7 ± 1.1 | 2.36 ± 0.13 | 14 | 0.520 ± 0.097 |
| 1984 | 16 | 0.480 ± 0.054 | 0.369 ± 0.038 | 4 | 15.3 ± 2.0 | 2.35 ± 0.03 | 15 | 0.540 ± 0.079 |

[a] Number of broods sampled.

rate decreased while tarsus growth rate was nearly constant; measurements at age 8 days declined from 1980 to 1981 (Table 2). From 1981 to 1982, growth rates increased while mass and tarsus length at age 8 days again declined. All parameters increased in 1983, but in 1984 growth rates declined, mass at age 8 increased, and tarsus length was constant. Clearly, 1983 was the most favorable year for Sage Sparrow growth; all parameters were at or near their greatest values. In 1982, growth rates were quite high, but mass and tarsus length at age 8 days were at their lowest levels.

For Brewer's Sparrows, only mass growth rate varied significantly among years (Table 1). Moreover, annual variation in Brewer's Sparrow mass growth rate did not parallel that of Sage Sparrows (Table 2); means were greatest in 1980 and 1982, and least in 1981. Evidently, either different factors caused annual growth variation in the two species, or they were influenced by the same factors in different ways.

Weather and food potentially cause annual variation in growth. Weather can influence growth directly through its effects on physiology or indirectly through its effects on food supply. Price (1985) documented annual variation in growth of Darwin's finches (*Geospiza fortis*) and attributed it to weather-mediated fluctuations in the food supply. Sage Sparrow annual mean tarsus growth rate varied inversely with mean daily maximum temperature during April and May ($r = -0.97$, df = 3) but not with mean daily maximum temperature during the brood-rearing portion of the breeding season (June–July, $r = -0.02$). Although we did not measure annual fluctuation in available foods, we did sample nestling diets in 1980–1983 (Petersen and Best 1986). Sage Sparrow annual mean mass growth rate varied with the percentage contribution of Lepidoptera larvae (the major food) to the diet ($r = 0.94$, df = 2, $P = 0.06$). Thus, some of the annual variation in Sage Sparrow growth may have resulted from effects of early-season temperatures on nestling foods. Annual variation in total precipitation was not significantly correlated with annual variation in Sage Sparrow growth. Brewer's Sparrow growth was not correlated with annual variation in any weather parameter.

*Seasonal variation.*—Sage Sparrow mass growth rate and tarsus length at age 8 days varied significantly among semimonthly periods of the breeding season (Table 1). Mass growth rate was high throughout June, but less for broods hatching in July; tarsus length at age 8 days declined slightly, but steadily, throughout the breeding season (Table 3). Brewer's Sparrow mass growth rate also varied among periods of the breeding season (Table 1). From early to late June, the mean growth rate constant increased; in early July, it was sharply reduced (Table 3). (Nearly all Brewer's Sparrow nesting was completed before late July.) Other investigators also have documented seasonal declines in growth parameters (e.g., Bryant 1978, Ricklefs and Peters 1979).

TABLE 3

SAGE AND BREWER'S SPARROW NESTLING GROWTH PARAMETERS (MEAN ± SD) THAT VARIED SIGNIFICANTLY AMONG SEMIMONTHLY PERIODS OF THE BREEDING SEASON

| | Sage Sparrow | | | | Brewer's Sparrow | |
|---|---|---|---|---|---|---|
| Period | Mass growth rate (K) | N[a] | Tarsus length at age 8 days (cm) | N[a] | Mass growth rate (K) | N[a] |
| 1–15 June[b] | 0.502 ± 0.052 | 23 | 2.38 ± 0.07 | 12 | 0.536 ± 0.092 | 19 |
| 16–30 June | 0.505 ± 0.060 | 26 | 2.34 ± 0.09 | 16 | 0.579 ± 0.070 | 28 |
| 1–15 July | 0.492 ± 0.088 | 38 | 2.31 ± 0.11 | 22 | 0.505 ± 0.068 | 19 |
| 16–31 July | 0.446 ± 0.052 | 13 | 2.25 ± 0.07 | 6 | | |

[a] Number of broods sampled.
[b] Each brood was assigned to one period, based on hatching date.

Several factors likely account for seasonal changes in growth. Daily maximum temperatures increased throughout the breeding season (early June: $\bar{x}$ = 20°C, late July: $\bar{x}$ = 30°C), and sparrow growth may have been inhibited by high temperatures in July (see also, Murphy 1985). Alternatively, seasonal fluctuations in potential nestling foods may have influenced growth. For example, seasonal variation in mass growth rate in both species roughly paralleled the abundance of sagebrush arthropods sampled by Winter (1984) in 1983. Both species forage heavily in sagebrush. Van Balen (1973) found a positive relationship between caterpillar density and asymptotic mass of Great Tits (*Parus major*). Similarly, Bryant (1975) documented a significant relationship between House Martin (*Delichon urbica*) growth and insect abundance. A third possible explanation for seasonal declines in growth is that adults become more taxed energetically as the season progresses (Morton et al. 1973, Biermann and Sealy 1985) and are unable to sustain high feeding rates.

*Effects of brood size.*—In general, brood size did not strongly influence Sage and Brewer's sparrow growth (Table 1); only two parameters varied significantly. For Sage Sparrows, tarsus growth rate was less in larger broods (b1: K = 0.406 ± 0.070, N = 7 broods; b2: 0.386 ± 0.051, N = 28; b3: 0.377 ± 0.050, N = 43; b4: 0.368 ± 0.036, N = 23); suggesting some limitation in the abilities of adults to provide food to larger broods. But tarsus length at age 8 days was not significantly related to brood size. Several investigators have documented negative effects of brood size on growth parameters (e.g., van Balen 1973, Bryant 1978). For Brewer's Sparrows, mass at age 7 days was significantly greater in larger broods (b2: $\bar{x}$ = 8.1 ± 3.2 g, N = 7; b3: 9.0 ± 0.7 g, N = 20; b4: 9.2 ± 0.8 g, N = 13); but because brood size interacted significantly with year and semi-

TABLE 4

SIGNIFICANT ($P \leq 0.01$) PARTIAL CORRELATIONS BETWEEN WEATHER VARIABLES AND SAGE SPARROW GROWTH RATE CONSTANTS (K) AND MEASUREMENTS AT AGE 8 DAYS (BROOD SIZE WAS CONTROLLED STATISTICALLY IN THE ANALYSIS)

| | K (df = 87) | | Measurements at age 8 days (df = 36) | |
|---|---|---|---|---|
| Weather variable[a] | Mass | Tarsus length | Mass | Tarsus length |
| TEMP | −0.29 | −0.33 | | −0.47 |
| TEMP1 | −0.30 | −0.30 | | −0.41 |
| TEMP2 | | | −0.48 | −0.47 |
| PRECIP | | | | 0.52 |
| PRECIP1 | | | | 0.48 |

[a] TEMP: mean daily maximum temperature over the entire nestling period; TEMP1: mean temperature over the first half (age 0–4 days) of the nestling period; TEMP2: mean temperature over the second half (>4 days) of the nestling period; PRECIP: total precipitation over the entire nestling period; PRECIP1: precipitation over the first half of the nestling period.

monthly period (Table 1), the effect of brood size was not consistent for all seasonal periods and all years (see also Best 1977).

*Effects of weather.*—When growth parameters for individual Sage Sparrow broods and their corresponding weather data were analyzed, a number of significant correlations emerged (Table 4). By contrast, Brewer's Sparrow growth was not correlated with weather, suggesting that either Brewer's Sparrows were more independent of environmental conditions or that conditions were more constant during their growth period. Brewer's Sparrows began nesting 1–2 weeks later and ended nesting about 2 weeks earlier than Sage Sparrows, but their nestlings did not encounter a narrower range of weather conditions.

Sage Sparrow growth rate constants and measurements at age 8 days were, in general, negatively correlated with temperature (Table 4). Precipitation was positively correlated with tarsus length at age 8 days, but precipitation was greatest early in the season when temperatures were cool. O'Connor (1977) and Murphy (1985) documented negative relationships between temperature and nestling size in the species they studied. Murphy suggested that heat stress resulting in mass loss was the primary reason for the relationship, but he also speculated that high temperatures may have impaired the ability of adults to forage and that assimilation efficiency may have decreased in extreme heat.

Weather seemed to influence growth more strongly early than late in the nestling period of individual broods. Four correlations (Table 4) involve weather effects in the first half of the nestling period (0–4 days of age), two in the second half (>4 days). This is not surprising as young

nestlings have poor thermoregulatory capabilities (e.g., Austin and Ricklefs 1977), whereas older nestlings, having developed endothermy, are better buffered from fluctuations in ambient temperature.

*Effects of ectoparasites.*—About 14% of all Sage Sparrow broods and 4% of all Brewer's Sparrow broods were parasitized by flesh fly larvae. For Brewer's Sparrows, fly parasitism did not significantly affect growth rate constants or mean mass or tarsus length at age 7 days. For Sage Sparrows, growth rate constants were not influenced by parasitism; however, parasitized broods had reduced tarsus lengths near the end of the nestling period. Mean values at ages 6 (1.93 ± 0.15 cm, N = 11 broods) and 7 days (2.12 ± 0.11 cm, N = 13) were significantly less than those for unparasitized broods (age 6 days: 2.04 ± 0.10 cm, N = 82, $t = 3.2$; age 7 days: 2.22 ± 0.10 cm, N = 72, $t = 3.3$); the mean value at age 8 days (parasitized: 2.24 ± 0.14 cm, N = 8; unparasitized: 2.32 ± 0.13 cm, N = 51; $t = 1.7$, $P = 0.10$) was nearly so. If reduction of nestling mass occurred, we could not detect it; larval biomass may have compensated for any mass lost by nestlings (see also Winterstein and Raitt 1983, Arendt 1985a). Young nestlings exhibited no reduction in size, but larval infestations usually were not evident until near the midpoint of the nestling period.

Nestling mortality attributable to fly parasitism was rare. Larvae usually evacuated just before nestlings fledged, and perhaps nestlings subsequently compensated for any previous reduction in growth. Gold and Dahlsten (1983), however, noted that stress at specific times may impede growth without the possibility of compensation even if the stress is later relieved. If growth reduction was not recovered, postfledging survival could have been reduced (see also Gold and Dahlsten 1983, Arendt 1985b).

*Conclusions.*—Growth in nestling Sage and Brewer's sparrows conforms to the general pattern documented for most passerines. Growth parameters were variable, and much of the variation in Sage Sparrow growth could be accounted for by differences among years, periods of the breeding season, and brood sizes, and by the effects of weather and ectoparasites. Overall, Brewer's Sparrow growth varied nearly as much as that for Sage Sparrows but was poorly explained by the variables that we measured. Food supply, an important component of the environment that we did not quantify, may have influenced growth in Brewer's Sparrows.

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# NEST-SITE CHARACTERISTICS AND REPRODUCTIVE SUCCESS OF LONG-EARED OWLS IN SOUTHWESTERN IDAHO

JEFFREY S. MARKS[1]

ABSTRACT.—In 1980 and 1981, I determined the outcome of 112 nesting attempts by 104 pairs of Long-eared Owls (*Asio otus*) in the Snake River Birds of Prey Area in southwestern Idaho. All nests were in trees in stick nests built by corvids. Owls used nests in clumps of trees and avoided nests in solitary trees and single rows of trees. Discriminant function analysis revealed that nests selected by owls tended to be wider than unused nests. Nesting success was 34% in 1980 and 51% in 1981. The minimum number of young fledged per successful nest was 3.4 in 1980 and 4.0 in 1981. Predators, probably raccoons (*Procyon lotor*), caused most nesting failures. Unsuccessful nests tended to be closer to water than were successful nests. Young owls left the nest about 2 weeks before they could fly and "branched" in the tree canopy surrounding the nest. "Branchers" had high survival, and branching may reduce nest predation. The number of nesting pairs in the study area declined 35% from 1980 to 1981. Nesting sites were more likely to have been reoccupied in 1981 if they had been successful in 1980. *Received 6 Dec. 1985, accepted 8 Apr. 1986.*

Long-eared Owls (*Asio otus*) inhabit temperate latitudes across North America and Eurasia (Burton 1973). Literature on their food habits is extensive (e.g., Marti 1976, Marks 1984). Because Long-eared Owls are almost strictly nocturnal and typically nest and roost in dense vegetation, much less is known about their breeding biology.

Breeding studies in Europe include Glue (1977), Nilsson (1981), Village (1981), Mikkola (1983), and Wijnandts (1984). The most extensive North American studies are from Arizona (6 nests, Stophlet 1959) and Idaho (20 nests, Craig and Trost 1979; 18 nests, Marks and Yensen 1980; 24 nests, Thurow and White 1984). Aside from Marks and Yensen (1980), I am not aware of any study that has assessed the influence of nest-site characteristics on nesting success.

Here, I report on nest-site characteristics and reproductive success of 104 Long-eared Owl pairs during 2 nesting seasons in the Snake River Birds of Prey Area (SRBPA) in southwestern Idaho. My main objectives were to (1) examine whether Long-eared Owls choose nest sites randomly, (2) determine if nest-site characteristics influence nesting success, and (3) present productivity data on nests that were followed from incubation until the young were capable of sustained flight.

[1] Montana Cooperative Wildlife Research Unit, Univ. Montana, Missoula, Montana 59812. (Present address: U.S. Bureau of Land Management, Boise District, 3948 Development Avenue, Boise, Idaho 83705.)

## STUDY AREA

The SRBPA comprises 338,778 ha of shrubsteppe desert in Ada, Canyon, Elmore, and Owyhee counties, southwestern Idaho. About 19% of the area is irrigated farmland. The native vegetation is dominated by big sagebrush (*Artemisia tridentata*) associations. Trees are confined primarily to riparian areas and farm settlements. Most of the native riparian trees are willows (*Salix* spp.). Russian olive (*Elaeagnus angustifolia*), black locust (*Robinia pseudoacacia*), and cottonwoods (*Populus* spp.) are the common exotics. Elevation at Long-eared Owl nests ranged from 740–875 m. A detailed description of the climate, vegetation, and topography of the SRBPA is available in U.S.D.I. (1979).

## METHODS

Field work began in late March each year and ended in late July in 1980 and in late August in 1981. I searched for owls along 115 km of the Snake River and 34 km of perennial tributaries. I also visited 5 tree groves that were isolated from the river. I used 9 × 35 binoculars to examine stick nests of Black-billed Magpies (*Pica pica*) and American Crows (*Corvus brachyrhynchos*) for the presence of owls. To minimize disturbance, I observed nests at a distance (usually >25 m) and tried to avoid flushing adults at nests. I obtained no data on clutch size or hatching success.

I considered a pair as breeding if I saw eggs, young, or a female owl in an incubation posture in a stick nest. A nest was considered disturbed if my presence caused a female to leave the nest.

Young Long-eared Owls leave the nest about 3 weeks after hatching to "branch" in the tree canopy near the nest (Craig and Trost 1979, Wijnandts 1984, pers. obs.). Owlets are flightless for about 2 weeks after leaving the nest. At about 5 weeks they begin to fly, at which time I considered them fledged. I defined a successful nest as one that fledged at least one young. When the nestlings were near branching age (again, based on my observations from a distance), I climbed to the nest to count and band them. I revisited the nest area repeatedly to search for branchers and ultimately to determine the number of fledglings produced.

I found some nests after the young had hatched. Data from these nests can inflate estimates of nesting success and productivity if early nesting failures are not detected (see Mayfield 1961). Thus, in addition to using all nesting attempts, I analyzed nesting success using (1) only the nests found during incubation, and (2) the Mayfield method (Mayfield 1961, 1975). I used a single estimate of success that combined the incubation and nestling periods (total of 56 exposure days) because survival rates did not differ between the 2 periods in either year ($\chi^2$ tests, $P > 0.30$; after Dow 1978).

I measured the following variables for each Long-eared Owl nest: (1) height (±0.1 m) of nest above ground, (2) height of nest relative to height of nest tree, (3) depth (±1 mm) of nest cup, (4) diameter (±1 mm) of nest cup at rim, (5) distance (±0.1 m) from nest to tree grove perimeter, (6) width (±0.1 m) of tree grove at nest, (7) distance (±1 m) to agriculture, (8) distance (±1 m) to road, and (9) distance (±1 m) to permanent water. I also measured nest height, nest depth, nest diameter, and distance to perimeter for each unused but apparently suitable corvid nest within 50 m of an occupied Long-eared Owl nest. Magpie nests with a complete canopy were considered unavailable to Long-eared Owls. I subjected variables from the 2 groups (occupied vs unused nests) to a stepwise discriminant function analysis (DFA) that maximized the Mahalonobis distance between groups (see Clark et al. 1983). This comparison provided a test of whether the physical characteristics of nests chosen by Long-eared Owls differed from those of nearby, unused nests. Owl nests that had no unused nests within 50 m were omitted from the analysis. I also used stepwise DFA to

compare the characteristics of successful vs unsuccessful Long-eared Owl nests. I used 2-tailed $t$-tests and pooled-sample variance estimates unless population variances were unequal.

## RESULTS

*Nesting density and clutch initiation.*—I found 63 nesting pairs in 1980 and 41 pairs in 1981. Although I probably did not find every nesting pair, I searched the study area with the same intensity each year.

Nesting densities were 0.42 pairs/km in 1980 and 0.28 pairs/km in 1981. The distance between adjacent owl nests ranged from 14 to 19,080 m ($\bar{x}$ = 1480 ± 2885 m [SD]). Perhaps because there were more nesting pairs, occupied nests were closer to one another in 1980 ($\bar{x}$ = 1253 ± 2598 m) than in 1981 ($\bar{x}$ = 1805 ± 3255 m), but the difference was not significant ($t$-test, $P = 0.32$). In 3 cases owls nested in colonies of 4 pairs; the closest nests were 16 m apart. One pair and 3 single birds that were not breeding occupied suitable nesting areas for about 2 weeks before moving elsewhere.

By backdating from estimated ages of nestlings and branchers, and by observations during the laying period, I estimated the initiation date for 85 clutches. Egg laying peaked during the last half of March in 1980 and during the first half of March in 1981 (Fig. 1). Seven of 18 clutches started after mid-April appeared to be renesting attempts (i.e., a pair was present at a nest site after loss of a clutch, and subsequently was observed with a new clutch). One pair renested twice. Most young fledged by late May in 1980 and by mid-May in 1981. I found no evidence that owls attempted to renest after a failure during brood-rearing.

*Nest-site characteristics.*—I recorded 112 nesting attempts including 8 renests. Seventy-nine nests were in old magpie nests and 33 were in old crow nests. Ninety-seven nests (87%) were in willow; the remainder were in Russian olive, black locust, black cottonwood (*Populus trichocarpa*), squawbush (*Rhus trilobata*), serviceberry (*Amelanchier alnifolia*), and tamarisk (*Tamarix chinensis*). At 50 sites, only open nests (i.e., crow nests or topless magpie nests) were available within 50 m of an owl nest. At the remaining 54 sites, one or more magpie nests with a partial canopy were present, and the numbers of open nests and partially-canopied nests were similar (79 vs 74, respectively). Owls nested in magpie nests with a partial canopy at 36 of these 54 sites (67%; proportion significantly >48%, $z$-test, $P = 0.01$).

Owl nests were usually near midheight in the nest tree and less than 4 m above ground (Table 1). Higher nests were not available at 8 of 14 sites where nests were <2 m above ground. Six nests were above 5 m. Owls did not nest in isolated trees or in single rows of trees, but only in clumps

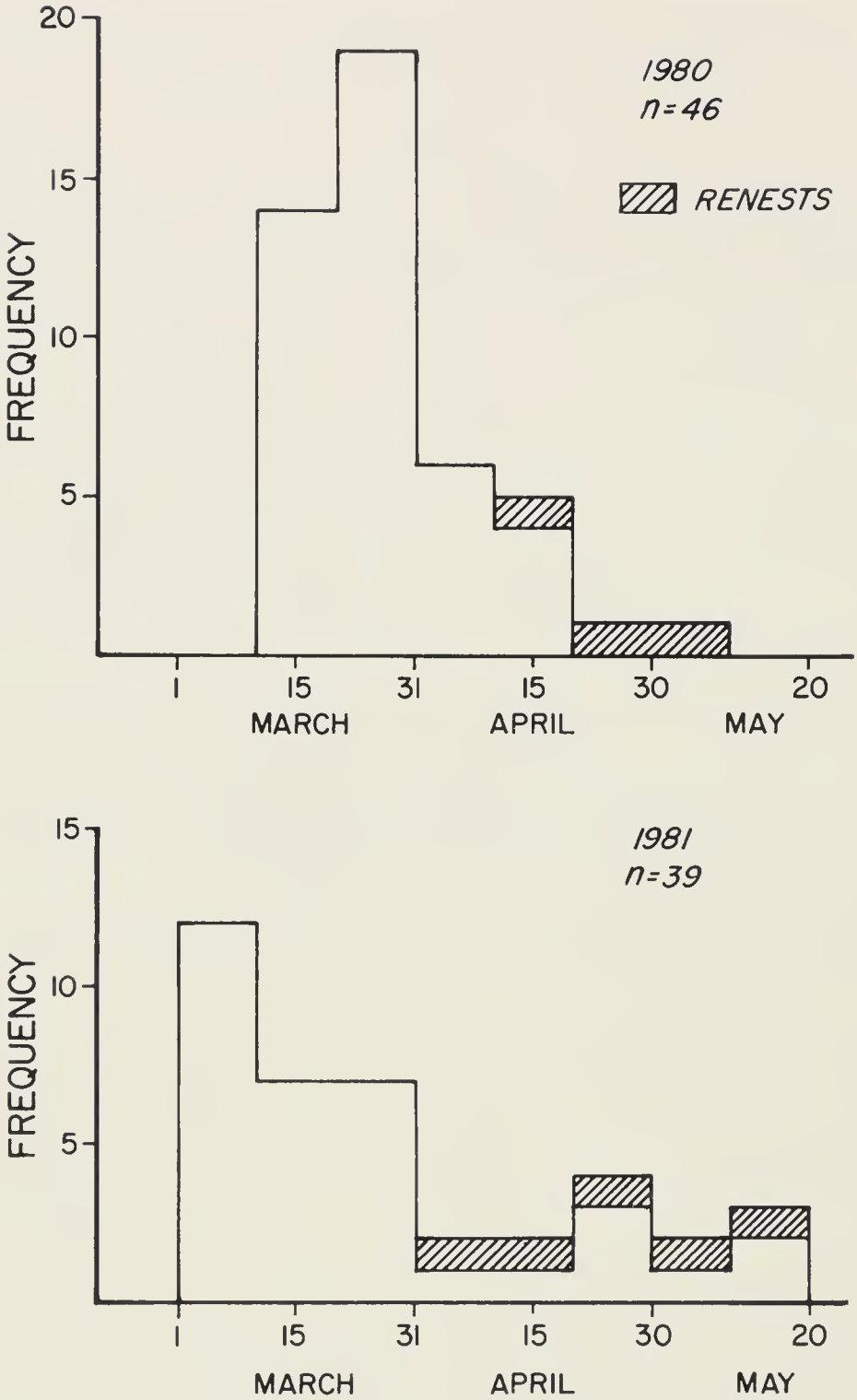


FIG. 1. Estimated date of initiation of Long-eared Owl clutches in the Snake River Birds of Prey Area, 1980–1981.

of trees. Eighty-six percent of all owl nests were in groves wider than 10 m. Owls often nested on the edge of clumps of trees, however, and 55% of the owl nests were within 5 m of the perimeter. The distances to roads and agriculture were highly variable (Table 1). Most trees grew near wet

TABLE 1
LONG-EARED OWL NEST-SITE CHARACTERISTICS IN THE SNAKE RIVER BIRDS OF PREY AREA, 1980–1981[a] (N = 112)

| | Mean ± SD | Range |
|---|---|---|
| Nest height (m) | 3.1 ± 1.2 | 1.3–8.1 |
| Relative height (%) | 49.4 ± 13.4 | 20.7–82.2 |
| Nest depth (mm) | 66.0 ± 31.0 | 5.0–180 |
| Nest diameter (mm) | 223.0 ± 32.0 | 152.0–302 |
| Distance to perimeter (m) | 6.6 ± 6.0 | 0.0–38.1 |
| Grove width (m) | 24.6 ± 19.5 | 5.0–99.0 |
| Distance to agriculture (m) | 651.0 ± 632.0 | 5.0–2240 |
| Distance to road (m) | 552.0 ± 630.0 | 4.0–2000 |
| Distance to water (m) | 143.0 ± 430.0 | 0.0–1900 |

[a] There was no significant difference in any nest-site characteristic between 1980 and 1981 ($t$-tests, $P > 0.05$).

areas, and 70% of the owl nests were within 25 m of permanent water. The large mean distance to water (143 m; Table 1) resulted from 6 nests in an isolated tree grove 1900 m from water. If these 6 nests are omitted, mean distance to water was 43 m.

Nest diameter, nest height, and nest depth contributed significantly in discriminating between owl nests and unused corvid nests within 50 m of an owl nest (Table 2). Group centroids were significantly different ($F$-test, $P < 0.001$), and the discriminant function classified 67.2% of the nests correctly. Corvid nests used by Long-eared Owls tended to be wider and slightly higher above ground than unused nests (Table 3) (Fig. 2). Unused nests were deeper than used nests. To test if nest depth was influenced by the presence of nestling owls (which may have trampled the nest), I compared mean nest depth of successful and unsuccessful nests. Successful nests were shallower than unsuccessful nests, but the difference was not significant ($t$-test, $P = 0.42$).

*Nesting success and productivity.*—Overall, nesting success was 40.9% in 1980 (N = 66) and 54.3% in 1981 (N = 46). Estimates of success based on nests found during incubation were about 5% lower, and, based on the Mayfield method, 10% lower than the overall estimates (Table 4). Steenhof and Kochert (1982) cautioned that the Mayfield method underestimates success if most of the unsuccessful nests are found. I found nearly 90% of the nests during the incubation period and determined the outcome of each nesting attempt. Thus, the figures obtained from nests found during incubation are probably the best estimates of nesting success.

The number of nestlings leaving the nest (branchers) was the same each

TABLE 2

DISCRIMINANT FUNCTION ANALYSIS COMPARING CORVID NESTS USED BY LONG-EARED OWLS AND UNUSED, SUITABLE NESTS

| Step | Variable entered[a] | Coefficient[b] | *P* |
|---|---|---|---|
| 1 | Nest diameter | 0.989 | 0.001 |
| 2 | Nest height | 0.344 | 0.001 |
| 3 | Nest depth | −0.189 | 0.001 |

[a] Distance to perimeter was not entered into the model.
[b] Standardized canonical discriminant function coefficient.

year (Table 5), but the fledging rate was higher in 1981 than in 1980. The number of young fledged per successful nest (both minimum and maximum) did not differ significantly between years (*t*-tests, $P > 0.10$). Most young that left the nest survived the 2-week branching period to become fledglings, and 96.3% of the nests with branchers were successful. Thirty-three (63%) of the successful nests fledged either 4 or 5 young, 2 nests fledged 6 young, and one nest fledged 7.

Of 60 nest failures, 58.3% occurred during incubation, 38.3% during brood-rearing, and only 2 nests (3.3%) failed after the young branched. The proportion of nests failing before or after hatching did not differ significantly between years ($\chi^2$ test, $P = 0.90$). Most failures appeared to be caused by predation. I found broken eggshells or partially eaten young at 33 nests. Eggs or young disappeared at 20 nests and were presumed depredated. Adults (probably females) were killed on the nest and nest contents destroyed in 3 cases. Two nests were abandoned, one clutch failed to hatch (Marks 1983), and one nest fell from the nest tree.

TABLE 3

MEANS FOR CHARACTERISTICS OF LONG-EARED OWL NESTS (N = 81) AND UNUSED, SUITABLE NESTS (N = 154) WITHIN 50 M OF AN OWL NEST

| | Nest site | | |
|---|---|---|---|
| | Used by owl | Not used | *P*[a] |
| Nest height (m) | 3.2 ± 1.2[b] | 2.9 ± 1.6 | 0.14 |
| Nest depth (mm) | 64.0 ± 28.6 | 67.0 ± 31.0 | 0.30 |
| Nest diameter (mm) | 223.0 ± 32.9 | 197.0 ± 29.1 | 0.001 |
| Distance to perimeter (m) | 6.4 ± 6.3 | 6.4 ± 6.4 | 0.98 |

[a] *t*-tests.
[b] Mean ± SD.

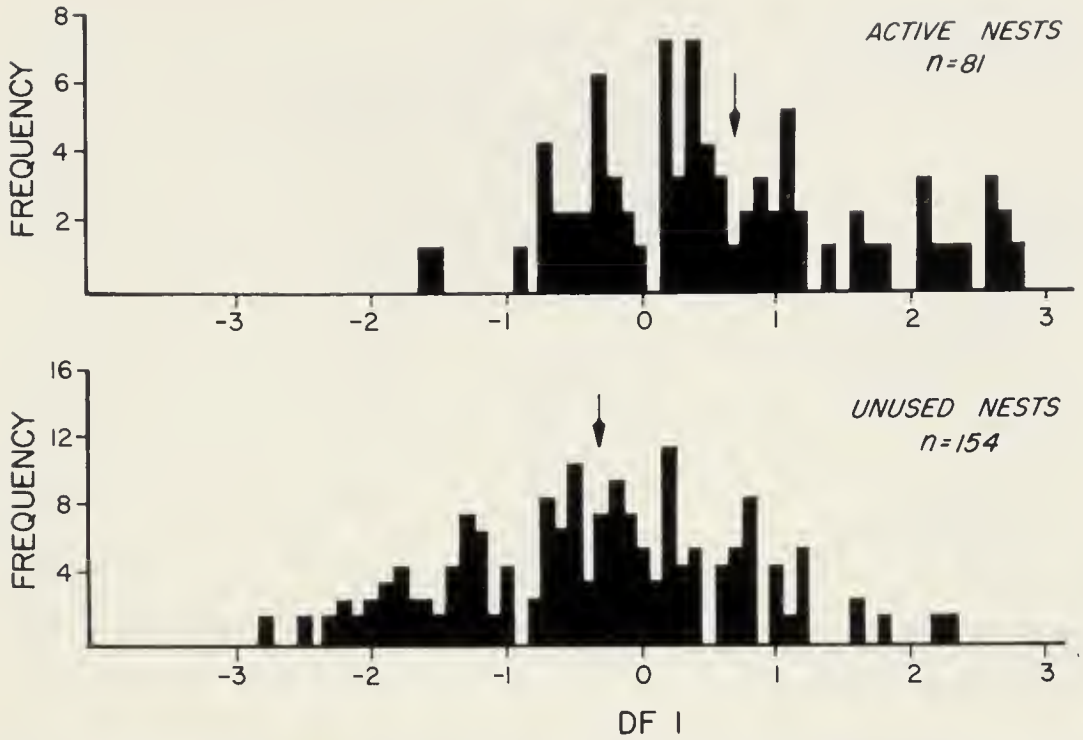


FIG. 2. Frequency distribution of scores for the first discriminant function comparing Long-eared Owl nests and nearby unused, apparently suitable nests. Arrows indicate group centroids. DF 1 is primarily a nest diameter-nest height axis. Owl nests are wider and slightly higher above ground than unused nests.

I believe that raccoons (*Procyon lotor*) were the major predators of Long-eared Owl nests in the SRBPA. I found raccoon tracks near several plundered nests and at one nest where an adult was killed. The remains of the other 2 adults were very similar to those attributed to raccoon predation. Other potential mammalian predators were either primarily terrestrial (e.g., canids and mustelids) or were rare in the area (e.g., bobcat [*Felis rufus*]). Great Horned Owls (*Bubo virginianus*) nested within 400 m of at least 6 Long-eared Owl nests, but I found no indication that they preyed on Long-eared Owls, nor have Long-eared Owls been found in samples of Great Horned Owl foods in the SRBPA (N = 796 prey items, unpubl. data). Amstrup and McEneaney (1980) saw a bull snake (*Pituophis melanoleucus*) kill and attempt to eat Long-eared Owl nestlings. These snakes are common in the SRBPA but feed almost exclusively on small mammals (Diller and Johnson 1982).

Successful nests were significantly farther from water ($\bar{x}$ = 247 ± 559 m) than were unsuccessful nests ($\bar{x}$ = 52 ± 244 m) ($t$-test, $P$ = 0.02). The height of successful nests ($\bar{x}$ = 3.2 ± 1.2 m) was nearly identical to that of unsuccessful nests ($\bar{x}$ = 3.1 ± 1.1 m).

Distance to water, nest diameter, and nest depth contributed signifi-

TABLE 4

LONG-EARED OWL NESTING SUCCESS BASED ON ALL NESTS, NESTS FOUND DURING INCUBATION, AND THE MAYFIELD METHOD

| | All nests[a] | Incubation[a] | Mayfield[b] |
|---|---|---|---|
| 1980 | | | |
| % success | 40.9 | 34.5 | 30.0 |
| 95% confidence interval | 29.0–52.8 | 22.3–46.7 | 20.0–44.0 |
| *N* | 66 | 58 | 62 |
| 1981 | | | |
| % success | 54.3 | 51.2 | 44.3 |
| 95% confidence interval | 39.9–68.7 | 35.9–66.5 | 30.0–65.0 |
| *N* | 46 | 41 | 40 |

[a] 95% CI from binomial distribution (Mosteller and Rourke 1973).
[b] 95% CI from Johnson (1979).

cantly in discriminating between successful and unsuccessful nests (Table 6) (Fig. 3). The group centroids were significantly different ($F$-test, $P < 0.05$), and the discriminant function classified 67.0% of the nests correctly.

*Human disturbance.*—During the incubation and early brood-rearing periods, female Long-eared Owls were on the nest every time I visited a nest during daylight hours. When disturbed by my approach, the female

TABLE 5

LONG-EARED OWL PRODUCTIVITY IN THE SNAKE RIVER BIRDS OF PREY AREA

| | 1980 | 1981 | Both years |
|---|---|---|---|
| No. nesting attempts | 66 | 46 | 112 |
| No. successful nests | 27 | 25 | 52 |
| No. branching young | 113 | 113 | 226 |
| No. branchers known dead | 5 | 5 | 10 |
| Min. no. fledglings[a] | 93 | 101 | 194 |
| Min. fledglings/successful nest | 3.44 | 4.04 | 3.73 |
| Min. fledglings/attempt[b] | 1.19 | 2.07 | 1.54 |
| Max. no. fledglings[c] | 108 | 108 | 216 |
| Max. fledglings/successful nest | 4.00 | 4.32 | 4.15 |
| Max. fledglings/attempt[b] | 1.38 | 2.21 | 1.72 |
| Min.–Max. % branchers fledged | 82–96 | 89–96 | 86–96 |

[a] Total number counted.
[b] Based on success rates of nests found during incubation.
[c] Includes missing branchers.

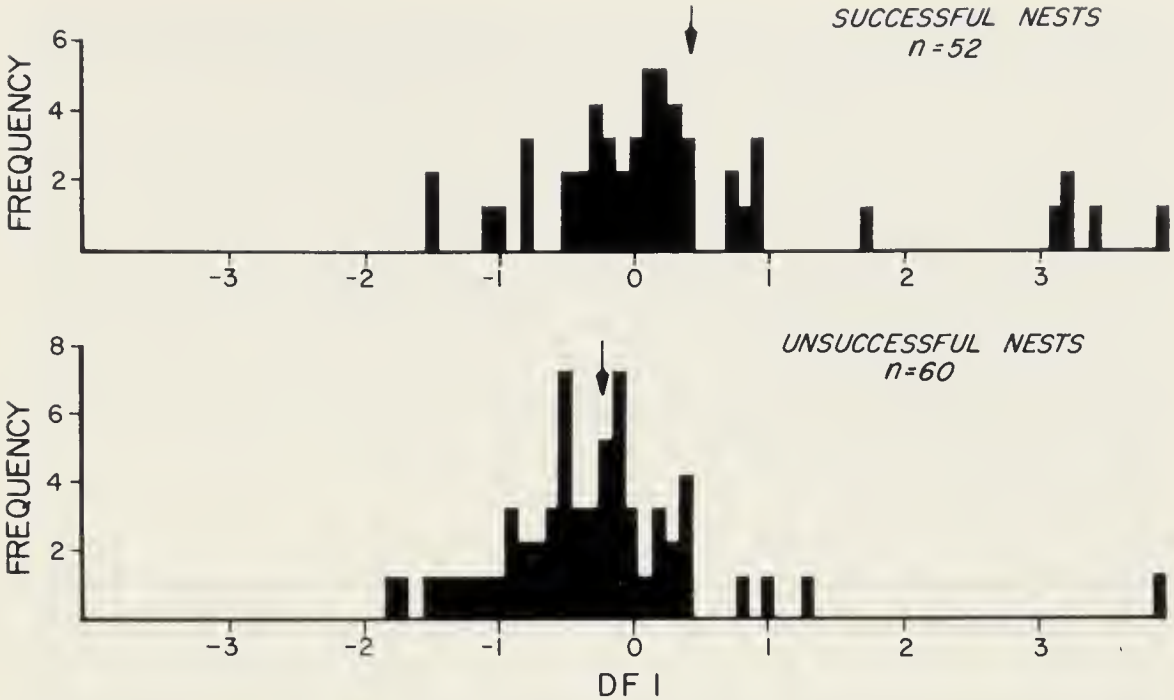


FIG. 3. Frequency distribution of scores for the first discriminant function comparing successful and unsuccessful Long-eared Owl nests. Arrows indicate group centroids. DF 1 is primarily a distance to water-nest diameter axis. Successful nests are farther from water and wider than unsuccessful nests.

usually resettled within 10 min after I left. Twice, I watched magpies remove eggs or hatchlings when I disturbed a nest at hatching. Sixty-five percent of the owl nests had at least one occupied corvid nest within 50 m; however, I never saw a corvid approach an owl nest when adults were present, and undisturbed nests probably were not vulnerable to corvid predation.

Although disturbed nests had lower success than undisturbed ones (31% vs 46%, respectively), nesting success was statistically independent of

TABLE 6

DISCRIMINANT FUNCTION ANALYSIS COMPARING SUCCESSFUL AND UNSUCCESSFUL LONG-EARED OWL NESTS

| Step | Variable entered | Coefficient[a] | *P* |
|---|---|---|---|
| 1 | Distance to water | 0.749 | 0.016 |
| 2 | Nest height[b] | — | — |
| 3 | Nest diameter | 0.507 | 0.037 |
| 4 | Nest depth | −0.461 | 0.050 |

[a] Standardized canonical discriminant function coefficient.
[b] Nest height was removed at step 5.

disturbance ($\chi^2$ test, $P > 0.10$). Mean distances to nearest road and to agriculture (both potential sources of disturbance) were not different for successful and unsuccessful nests ($t$-tests, $P > 0.50$).

*Reoccupation of nesting sites.*—In 1981, nesting owls occupied 30 of 63 sites (48%) that were used in 1980. I found 11 new sites in 1981. Seventy-four percent of the nests that were successful in 1980 were reoccupied in 1981, whereas only 28% of the nests that failed were reoccupied in 1981 ($\chi^2$ test, $P < 0.001$). Three of 4 males banded as nestlings and captured as breeders a year later nested at sites that were occupied in their natal year (see Marks 1985). Disturbance at a nest in 1980 had no effect on reoccupancy in 1981 ($\chi^2$ test, $P > 0.20$).

## DISCUSSION

*Nesting density and chronology.*—Nesting densities in the SRBPA (0.28–0.42 pairs/km) were lower than those in southeastern Idaho (0.64 pairs/km, Craig and Trost 1979) and south-central Idaho (1.55 pairs/km$^2$, Thurow and White 1984) but higher than densities elsewhere in North America (e.g., Craighead and Craighead 1956, Stophlet 1959, Smith and Murphy 1973, Knight and Erickson 1977) or in Europe (Wijnandts 1984:12). Nesting densities are not always comparable among study areas owing to differences in availability of suitable nesting habitat. For example, much of the riparian zone in the SRBPA was treeless, whereas in south-central Idaho, Long-eared Owls nested in a continuous block of sagebrush-juniper ecotone (Thurow and White 1984). My data support those of Craig and Trost (1979) and Thurow and White (1984) in showing that Long-eared Owls are common in the shrubsteppe desert of southern Idaho.

On average, owls laid eggs a month earlier in the SRBPA than in southeastern or south-central Idaho, where all eggs were laid in April or May (Craig and Trost 1979, Thurow and White 1984). Both of these latter study areas were at higher elevations than the SRBPA.

*Nest sites and reproductive success.*—Throughout their range, Long-eared Owls nest in stick nests in trees (Burton 1973). Occasionally, they nest in tree cavities (Craighead and Craighead 1956), cliffs (Marks and Yensen 1980), and on the ground (Bent 1938, Mikkola 1983). I found no evidence that Long-eared Owls construct new nests or modify old ones (see Glue 1977, Craig and Trost 1979).

Long-eared Owls are cryptically colored, have well-developed ear tufts (see Perrone 1981), and typically remain still when potential predators approach. Camouflage is probably their primary means of avoiding predators, and owls may enhance their crypticity through nest-site selection. Owls clearly did not select nests at random. Owls nested in clumps of trees that provided more cover for nesting and roosting adults, and for

branching young than would have been available in solitary trees or single rows of trees. Nests with a partial canopy offer additional concealment, and they were preferred over open nests in the SRBPA and in Craig and Trost's (1979) study area. Owls also preferred wide nests, which seemed to provide ample room for eggs or nestlings and would probably help conceal females from ground-based predators. The tendency for owls to nest near the edge vs the center of clumps of trees probably reflected availability, as most corvid nests were near the periphery of a tree grove.

Raccoons obtain most of their food from wetlands (Fritzell 1978, Greenwood 1982), and in arid areas they frequent riparian habitat (pers. obs.). This probably explains why distance to water was the best predictor of nesting success of owls in the SRBPA. Although nest height was not a good predictor of nesting success (but see Marks and Yensen 1980), the highest nests (those >5 m) never were destroyed by predators, and there may be a height threshold above which Long-eared Owl nests are relatively safe from mammalian predators.

Compared with data from other studies, nesting success appeared to be low in the SRBPA (34.5–51.2%). Nesting success was 83.3% in Arizona (Stophlet 1959), 84.2% in southeastern Idaho (Craig and Trost 1979), and 100% in south-central Idaho (Thurow and White 1984). The number of young fledged per successful nest was similar among study areas. Long-eared Owls nesting in the SRBPA apparently were more vulnerable to nest predators than were owls in the other study areas. Nests in Arizona were high above ground (5–16 m), and those in south-central Idaho were in junipers on upland sites. These nests would have been less vulnerable to raccoons than were nests in the SRBPA. Nests in southeastern Idaho were close to the ground ($\bar{x}$ = 2.2 m) and near a river, but raccoons were not observed in the study area (T. H. Craig, pers. comm.).

*The adaptive significance of branching.*—Many observers have noted that Long-eared Owl young leave the nest long before they can fly (e.g., Whitman 1924, Sumner 1929, Armstrong 1958). Sumner (1929) believed that branching was a liability because it exposed young owls to predators. Survival of branchers was high in the SRBPA, however, and all but 2 nests with branchers were successful. I suggest that branching acts to reduce predation. Werschkul (1979) argued that the escape response of nestling Little Blue Herons (*Egretta caerulea*) reduced their vulnerability to predators. Trees refoliated in the SRBPA at about the same time that the first branchers appeared. Branchers were solitary and well-concealed by foliage. Even a single nestling would benefit from branching because occupied nests might serve as visual or olfactory cues to mammalian predators.

*Fidelity to nesting sites.*—In parts of Europe, Long-eared Owl popula-

tions fluctuate with microtine rodent cycles (Hagen 1965, Källander 1977, Lundberg 1979, Village 1981). The Long-eared Owl-microtine relationship has not been documented in North America, although Marti (1974) and Craig and Trost (1979) considered Long-eared Owls to be nomadic on their study areas in Colorado and Idaho, respectively. Craig and Trost (1979) suggested that weather influenced breeding, with fewer pairs nesting during a cool, wet spring. The 35% decline in the number of nesting pairs from 1980 to 1981 in the SRBPA cannot be explained by either of the above mechanisms. Long-eared Owls in the SRBPA fed primarily on noncyclic rodents (i.e., cricetids and heteromyids), and food habits were very similar in the 2 years (Marks 1984). The spring of 1981 was wetter than in 1980, but owls nested almost 2 weeks earlier in 1981 than in 1980.

For a variety of nonpasserines, studies of marked individuals have shown that nesting sites are more likely to be reoccupied in years following successful nesting attempts and abandoned after nesting failures (e.g., Newton and Marquiss 1982, Picozzi 1984). If nomadism occurs in Long-eared Owls, it may be related to nest predation rather than to food availability or weather. Sonerud (1985) came to a similar conclusion in explaining nest-hole shifts in Tengmalm's Owls (*Aegolius funereus*) in Norway.

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## 1987 ANNUAL MEETING

The WILSON ORNITHOLOGICAL SOCIETY will hold its 68th annual meeting at Utica College of Syracuse University from 27 to 31 May 1987. The event will be a joint meeting with the Eastern Bird Banding Association and will be hosted by Utica College together with the Kirkland and Oneida Bird Clubs. JUDITH W. McINTYRE, Utica College, Utica, New York 13502, is chairing the Local Committee. JON C. BARLOW, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Canada M5S 2C6, is chairing the Program Committee and invites suggestions for symposia.

There will be two special exhibits: (1) a reception will be given on Friday night by the Munson-William-Proctor Institute of Utica for their special exhibit of Birds in Art, and (2) Karen Allaben-Confer, winner of the first George Miksch Sutton Award from the Wilson Ornithological Society will exhibit her most recent work in the Barrett Art Gallery at Utica College.

Field trips planned include a trip to a bog, local birding, a mushroom walk, and a journey to the Oneida Community. Sunday field trips will include the Adirondack Park and a surprise birding adventure led by Susan Drennan, author of "Where to Find Birds in New York State." A circular of information and a call for papers will be distributed shortly.

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# RED-TAILED HAWK NEST SITES IN PUERTO RICO

EDUARDO SANTANA C.,[1,2] EDDIE N. LABOY,[3] JAMES A. MOSHER,[4] AND STANLEY A. TEMPLE[1]

ABSTRACT.—We describe Red-tailed Hawk (*Buteo jamaicensis*) nest sites in four habitats in Puerto Rico. Forty-nine nests were located in 21 species of trees. Red-tailed Hawks nested in trees that were taller than the mean canopy height of trees in surrounding plots and that allowed a view of at least 50% of their territory. Most nests were in the upper third of the tree on horizontal branches and secondary crotches. Vines and epiphytes commonly supported nests. Differences in nest-site parameters among different habitat types reflected major dissimilarities in vegetation, topography, climate, and land-use patterns. Nest plots in the dry lowlands were farther from water, had fewer species of trees, and shorter nest trees than nest plots in the other habitat types. Because they occurred mostly in grazed or recently abandoned pastures, nest plots in the dry lowlands also had less-developed shrub layers and greater ground cover. Like their continental North American counterparts, Red-tailed Hawks in Puerto Rico nested in sites that offered a wide view of the territory. *Received 21 Oct. 1985, accepted 2 June 1986.*

RESUMEN.—Describimos los sitios de anidamiento del Guaraguao en cuatro hábitats en Puerto Rico. Cuarenta y nueve nidos fueron encontrados en 21 especies de árboles. Los Guaraguaos anidaron en árboles que eran mas altos que la altura promedio del dosel y esto les permitió tener una visibilidad desde el nido de mas del 50% de su territorio. La mayoría de los nidos se encontraron en el parte superior del árbol sobre ramas horizontales y horquetas secundarias. Comunmente los nidos se encontraron apoyados sobre bejucos y plantas epífitas. Las diferencias observadas entre los sitios de anidamiento en los diferentes hábitats reflejaron las diferencias generales entre las zonas de estudio con respecto a vegetación, topografía, clima y patrones del uso de la tierra. Los sitios de anidamiento en las zonas áridas a baja altitud se encontraron mas lejos del agua, tenían menos especies de árboles y tenían árboles de menor estatura que los sitios de anidamiento en los otros hábitats. Por su localización en pastizales y potreros abandonados los sitios de anidamiento en las zonas áridas tenían un estrato arbustivo menos desarrollado y una mayor cubierta vegetal del suelo que los sitios de anidamiento en los otros hábitats. Al igual que los Guaraguaos en América del Norte los Guaraguaos en Puerto Rico anidaron en sitios que ofrecían una vista amplia del territorio.

The nesting habits of Red-tailed Hawks (*Buteo jamaicensis*) in temperate North America have been well described (e.g., Bent 1937, Hagar 1957, Belyea 1976, Howell et al. 1978, Petersen 1979, Titus and Mosher 1981, Bednarz and Dinsmore 1982), but little is known about their nesting habits in the one-quarter of the latitudinal extent of their range that lies

[1] Dept. Wildlife Ecology, Univ. Wisconsin, Madison, Wisconsin 53706.
[2] Institute of Tropical Forestry, Southern Forest Experiment Station, P.O. Box AQ, Rio Piedras, Puerto Rico 00928.
[3] Departamento de Recursos Naturales, Jobanes, Apartado 327, Guayama, Puerto Rico 00655.
[4] Savage River Consulting, P.O. Box 71, Frostburg, Maryland 21532.

within the tropics. Here, we present information on Red-tailed Hawk nest sites in four tropical habitats in Puerto Rico at the southeasternmost limit of the geographic range of the species.

## STUDY AREA

Puerto Rico is the smallest (8900 km$^2$) and easternmost island of the Greater Antilles. Approximately 22% of the island has slopes greater than 45%, and it has mountain peaks of up to 1340 m. By 1912 less than 1% of the virgin forests of Puerto Rico remained, and much of the land was converted to pastures and agriculture (Wadsworth 1949). More recently, agricultural activities have declined, and lands have reverted back to forest. Presently, about 30% of the island is classified as forest (Birdsey and Weaver 1982).

We studied the Puerto Rican Red-tailed Hawk (*B. j. jamaicensis*) or "Guaraguao" in four distinct habitats: dry lowlands, moist lowlands, montane rain forest, and montane cloud forest. The dry-lowland study area (altitude range: 0–200 m above sea level) was in southwestern Puerto Rico within the subtropical dry-forest life-zone (Ewel and Whitmore 1973), and it consists primarily of pastures with scattered trees and shrubby areas. Mean annual rainfall is about 90 cm, and mean monthly temperature varies from approximately 23.9 to 28.4°C.

The moist lowland study areas (0–450 m above sea level) were in central and northeastern Puerto Rico at low- and mid-elevations within the subtropical-moist and wet-forest life-zones (Ewel and Whitmore 1973). This habitat is dominated by pastures, small agricultural plots, and patches of secondary forests interspersed along ravines and ridges. Mean annual rainfall varies from about 100 to 300 cm, and mean monthly temperature varies from approximately 20.5 to 27.0°C.

The montane rain-forest and cloud-forest study areas (450–1050 m above sea level) were located within the rugged 11,200-ha Luquillo Experimental Forest in northeastern Puerto Rico. This forest reserve contains the largest expanses of primary forests remaining on the island. Mean annual rainfall is about 400 cm, and mean monthly temperature varies from approximately 19.2 to 25.0°C. At lower elevations the forest canopy reaches heights of approximately 20 m and is comprised of over 150 species of trees. Canopy height and tree species diversity decrease with increasing altitude, and a stunted cloud forest occurs near the summits of the mountains.

The cloud-forest study area was found within the lower-montane rain-forest life-zone (Ewel and Whitmore 1973). Here, high winds are common, and fog reduces solar radiation by 40% (Howard 1970). Mean annual rainfall is about 400 cm, and mean monthly temperature varies from approximately 16.7 to 21.0°C.

## METHODS

Field work was conducted from August 1981 to July 1983. We found nests in the lowlands by visiting nest sites reported to us by local residents and by systematically searching for nests along roads. In the rain and cloud forests we climbed emergent trees, cliffs, and observation towers that offered a view above the canopy, and we visually followed adult Red-tailed Hawks that were carrying prey or twigs to their nests.

We sampled the vegetation on nest plots using the methods described by Titus and Mosher (1981), as modified from James and Shugart (1970). Each nest plot consisted of a 0.04-ha circular plot (11.3 m radius) with the nest tree at its center. Table 1 presents a description of the 22 variables measured within each nest plot. Variables 1–4 describe the nest location and the nest tree, variables 5–7 describe distances between the nest tree and specific habitat

TABLE 1

DESCRIPTION OF THE VARIABLES MEASURED AT RED-TAILED HAWK NEST-SITE PLOTS IN PUERTO RICO

| Mnemonic code | Description of variable (units) |
|---|---|
| 1. NEST HT | Height of nest (m). |
| 2. HT NST TREE | Height of nest tree (m). |
| 3. P NST HT | Nest height as % of tree height. |
| 4. DBH | Diameter at breast height of nest tree (cm). |
| 5. DIS H2O | Distance to nearest permanent freshwater body (m). |
| 6. DIS FOR OP | Distance to nearest forest opening (m). |
| 7. DIS HUM | Distance from human activity (e.g., houses, roads well-traveled by pedestrians, areas where humans are active >8 h per day) (m). |
| 8. CAN HT | Average canopy height of the plot (m). |
| 9. NO TREES | Number of overstory trees (those trees with crowns at the canopy level). |
| 10. NO SP TREE | Number of species of overstory trees. |
| 11. SHRUB DEN | Shrub density (James and Shugart 1970). |
| 12. SHRUB IND | Shrub index, measured along the same transect as SHRUB DEN, except all woody stems 1–6 cm diameter and 0.25–1.75 m in height are measured; includes SHRUB DEN plus shrubs that do not intersect outstretched arms. |
| 13. CAN TOT[a] | Percentage total canopy cover. |
| 14. UND TOT[a] | Percentage total understory tree (trees with crowns below the canopy level) cover. |
| 15. GRND TOT[a] | Percentage total ground cover (any green vegetation <1 m tall). |
| 16. UND 14 | Number of understory stems in the plot with diameter between 1 and 4 cm. |
| 17. UND 58 | Number of understory stems 5–8 cm in diameter. |
| 18. UND GT9 | Number of understory stems with diameter >9 cm. |
| 19. DBH LT25 | Number of overstory trees in the plot with dbh <25 cm. |
| 20. DBH 2650 | Number of overstory trees with dbh between 26 and 50 cm. |
| 21. DBH GT50 | Number of overstory trees with dbh >50 cm. |
| 22. BASAL | Basal area in $m^2$/ha for overstory trees. |

[a] Mean values based on 40 ocular tube readings, 10 along each of the 4 transects used in SHRUB DEN (James and Shugart 1970).

features, and variables 8–22 describe the vegetation structure. All distances were measured using a Haga altimeter, tape measure, or range finder. We recorded the location of the nest on the tree (e.g., main crotch, horizontal branch, etc.), the position of the nest tree relative to topographic features (e.g., upper or lower half of hill, ridgetop, hollow, etc.), and the directional exposure of the slope (0° = north). We mapped the boundaries of 33 Red-tailed Hawk territories during the breeding season by observing courtship and territorial displays of adults that we recognized by plumage characteristics and by the nest sites they returned to after interacting with neighboring birds. We estimated the proportion of each territory that could be viewed from each nest by climbing to the nest or to a nearby tree and subjectively classifying each nest as allowing a view of <50% or >50% of the territory.

TABLE 2
FREQUENCY OF VINES AND EPIPHYTES AT RED-TAILED HAWK NESTS IN DIFFERENT HABITATS IN PUERTO RICO

| Study area | Number of nests | % nests in contact with vines[a] | % nests supported by vines[b] |
|---|---|---|---|
| Dry lowland | 6 | 33 | 0 |
| Moist lowland | 18 | 61 | 28 |
| Cloud and rain forest | 10 | 90 | 70 |

[a] Differences among study areas were not statistically significant ($\chi^2 = 5.51$, df = 2, $0.05 < P < 0.10$).
[b] Differences among study areas were statistically significant ($\chi^2 = 8.94$, df = 2, $P < 0.025$).

## RESULTS

We found 49 nests and measured vegetation parameters on 6 nest plots in the dry lowlands (altitude range: 5–40 m), 30 in the moist lowlands (5–402 m), 2 in the rain forest (490–650 m), and 2 in the cloud forest (750–870 m). The 15 nests described by Laboy (1982) in moist-lowland habitat are included in our sample. We were unable to measure vegetation parameters for 9 of the 49 nests, but we did obtain other information on their nest-site characteristics, which was used in the analyses.

The 49 nests were in 21 species of trees; 8 were in *Hymenaea courbaril,* 6 were in *Cecropia peltata,* 6 were in *Bucida buceras,* 5 were in *Casuarina equisetifolia,* and 3 were in *Spondias mombin.* Forty-seven percent of these nests were located on horizontal branches, 27% on secondary crotches, 20% on the main crotch, and 6% were braced against the trunk. Eighty percent of 40 nests were in the upper third of the tree. In 76% of 33 plots that contained three or more trees, Red-tailed Hawks selected a tree taller than the average canopy height of the plot ($\chi^2 = 10.94$, df = 1, $P < 0.05$).

Ten species of vines and epiphytes were in contact with 65% of 34 nests and were an important source of support for 29% of the nests (Table 2). Three nests were completely supported by vines or epiphytes and did not touch branches of the nest tree. The incidence of vines and epiphytes at nests increased progressively from dry to wet habitats (Table 2). In the rain and cloud forests 70% of the nests were not visible from the ground due to the screening effect of vines. Vines and epiphytes in contact with nests included *Paullinia pinnata* (Sapindaceae), *Securidaca virgata* (Polygalaceae), *Odontosoria aculeata* (Polypodiaceae), *Macfadyena unguis-cati* (Bignoniaceae), *Philodendron oxycardium* (Araceae), *Symphysia racemosa* (Ericaceae), *Schlegelia brachiantha* (Scrophulariaceae), *Clusia gundlachii* (Clusiaceae), *Marcgravia sintenisii* (Marcgraviaceae), and *Guzmania* sp. (Bromeliaceae).

Fifty-three percent of the nest trees were on the upper half of a hill, 22% on the lower half or in the bottom of a valley, and 25% in flat areas. In 82% of 33 nests an adult at the nest could view >50% of its territory. The hillsides where the nests were located did not face any particular direction ($\chi^2 = 9.04$, df = 7, $P > 0.05$). Thirty-six percent of 35 nests in our dry-lowland and moist-lowland study areas were within 300 m of human activity; one was 29 m away from a house. Only one of 16 nests that were inspected in two consecutive breeding seasons was reused.

Nest plots in the dry lowlands were farther from water, had fewer species of trees, and shorter nest trees than nest plots in the other habitat types (Table 3). Because they occurred mostly in grazed or recently abandoned pastures, nest plots in the dry lowlands also had less-developed shrub layers and greater ground cover. The high values of NEST HT, HT NST TRE, DBH, and CAN HT for the rain-forest plots probably reflected the abundance of tall trees in that habitat. The low number of nest plots in the rain and cloud forest did not allow us to compare them statistically with nest plots in the other habitat types.

## DISCUSSION

Techniques developed in temperate North America for nest-site habitat analysis worked fairly well in Puerto Rico, but a few problems were encountered. In some nest plots the crown of the nest tree covered the entire 0.04-ha plot, accounting for 100% canopy cover. Many of the stems we tallied in moist-lowland, rain-forest, and cloud-forest plots were actually woody lianas hanging down from the canopy of the nest tree. Measuring the diameter, angle, and number of branches supporting the nest was often meaningless because of the presence of numerous vines and epiphytes that also offered support to the nest.

Differences in nest-site parameters among the different habitat types (Table 3) reflected major dissimilarities in vegetation, topography, climate, and land-use patterns. Santana and Temple (in press) found that the percent coverage of pastures within Red-tailed Hawk territories was 84%, 47%, 0%, and 0% in the dry-lowland, moist-lowland, rain-forest, and cloud-forest habitats, respectively. Whereas, the percent coverage of shrubland and forest was 10%, 43%, 99%, and 99%, respectively. Nest-site characteristics reflected these general landscape differences. Mosher et al. (1986) and Titus (1984) have shown for other species of raptors that nest-site habitat differences among regions are partly due to differences in the structure of available habitat in each region.

Unlike their temperate-zone counterparts, hawks in the humid tropics commonly use vines and epiphytes as a source of support for their nests (Wiley and Wiley 1981, Delannoy 1984, Griffin 1985). The incidence of

TABLE 3

RED-TAILED HAWK NEST-SITE CHARACTERISTICS IN FOUR DIFFERENT HABITATS IN PUERTO RICO

| Variable | Dry lowland | Moist lowland | Rain forest | Cloud forest |
|---|---|---|---|---|
| NEST HT | 9.9 ± 3.7 (6)[a] | 14.9 ± 7.0 (30) | 21.6 ± 1.5 (2) | 13.2 ± 1.4 (2) |
| HT NST TREE | 12.3 ± 3.4 (6)[b] | 18.4 ± 6.8 (30) | 26.6 ± 1.0 (2) | 19.8 ± 1.1 (2) |
| P NST HT | 76.6 ± 14.5 (6) | 79.2 ± 14.6 (30) | 81.9 ± 9.0 (2) | 66.8 ± 10.7 (2) |
| DBH | 66.2 ± 18.7 (6) | 73.7 ± 34.3 (30) | 94.9 ± 5.8 (2) | 51.2 ± 6.6 (2) |
| DIS H2O | 427.3 ± 291.9 (6)[c] | 166.3 ± 160.3 (31) | 38.0 ± 11.3 (2) | 46.5 ± 64.3 (2) |
| DIS HUM | 667.7 ± 475.3 (6) | 475.5 ± 433.1 (29) | 917.0 ± 1060.7 (2) | 1773.5 ± 327.6 (2) |
| DIS FOR OP | 33.3 ± 57.7 (3) | 31.9 ± 35.9 (26) | 96.0 ± 5.6 (2) | 100.0 ± 0.0 (2) |
| CAN HT | 10.2 ± 0.6 (3)[c] | 15.8 ± 5.1 (26) | 20.2 ± 0.3 (2) | 13.2 ± 4.4 (2) |
| NO TREES | 3.3 ± 3.0 (6) | 8.1 ± 6.7 (31) | 7.5 ± 0.7 (2) | 18.0 ± 14.1 (2) |
| NO SP TREE | 1.5 ± 0.8 (6)[c] | 3.4 ± 1.7 (31) | 5.5 ± 0.7 (2) | 5.5 ± 3.5 (2) |
| SHRUB DEN | 9.7 ± 12.9 (6)[c] | 47.5 ± 28.8 (30) | 23.5 ± 4.9 (2) | 26.5 ± 2.1 (2) |
| SHRUB IND | 29.2 ± 35.8 (6)[b] | 83.9 ± 48.6 (30) | 38.0 ± 0.7 (2) | 50.0 ± 2.8 (2) |
| CAN TOT | 57.3 ± 23.5 (6) | 74.1 ± 20.2 (30) | 99.0 ± 0.7 (2) | 94.0 ± 8.5 (2) |
| UND TOT | 34.0 ± 29.4 (6)[c] | 70.1 ± 28.2 (30) | 87.0 ± 9.9 (2) | 80.0 ± 0.0 (2) |
| GRND TOT | 90.5 ± 12.7 (6)[b] | 69.9 ± 19.5 (30) | 65.0 ± 24.0 (2) | 84.0 ± 0.0 (2) |
| UND 14 | 22.2 ± 25.4 (6)[b] | 80.7 ± 52.5 (30) | 55.0 ± 9.9 (2) | 38.5 ± 19.1 (2) |
| UND 58 | 4.5 ± 8.4 (6) | 9.7 ± 8.4 (30) | 19.0 ± 4.2 (2) | 19.0 ± 7.1 (2) |
| UND GT9 | 0.7 ± 1.2 (6)[b] | 4.3 ± 4.0 (30) | 30.5 ± 6.4 (2) | 14.0 ± 2.8 (2) |
| DBH LT25 | 1.5 ± 2.5 (6) | 4.7 ± 5.7 (30) | 3.0 ± 0.0 (2) | 13.5 ± 12.0 (2) |
| DBH 2650 | 1.0 ± 0.9 (6) | 2.7 ± 2.7 (30) | 2.5 ± 0.7 (2) | 2.0 ± 0.0 (2) |
| DBH GT50 | 0.8 ± 0.8 (6) | 1.4 ± 1.3 (30) | 2.0 ± 0.0 (2) | 2.5 ± 2.1 (2) |
| BASAL | 15.1 ± 11.1 (6) | 30.7 ± 19.2 (30) | 37.6 ± 0.6 (2) | 32.0 ± 19.6 (2) |

[a] $\bar{x}$ ± SD ($N$).
[b] Dry lowlands and moist lowlands significantly different at $P < 0.05$ using a 2-tailed $t$-test.
[c] Dry lowlands and moist lowlands significantly different at $P < 0.01$ using a 2-tailed $t$-test.

vines and epiphytes at nest sites in our study areas paralleled the abundance of these plants in the environment (Richards 1952). Vines provide support for nests in trees that may otherwise lack adequate support, and they make the nest less conspicuous. The evergreen condition of the canopy and the abundance of vines and epiphytes make it difficult to find nests in humid tropical forests.

A lower percentage of nests was reused in consecutive years in Puerto Rico (6%) than in North America (17–50%) (Orians and Kuhlman 1956, Hagar 1957, Seidensticker and Reynolds 1971, Belyea 1976, Bohm 1978). This might be due to the abundance of nest sites in our study areas or to fast rates of nest decomposition. Dead branches and leaves in the canopy of tropical rain forests have been shown to decompose at rapid rates (Frangi and Lugo 1985); similar rapid decomposition of nest materials might reduce the rate of nest reuse.

Puerto Rican Red-tailed Hawks used a greater variety of tree species for nesting (ratio of tree species used to nests = 0.43) than do Red-tailed Hawks in North America (range of ratio = 0.03–0.38) (Bent 1937, Gates 1972, Belyea 1976, Mader 1978, Titus and Mosher 1981, Bednarz and Dinsmore, 1982), probably reflecting the higher diversity of tree species in Puerto Rico (Little et al. 1974). The most commonly used tree species (*Bucida buceras, Hymenaea courbaril, Casuarina equisetifolia, Cecropia peltata*) were also very common in their respective habitats (Birdsey and Weaver 1982). Due to their growth form, size, and location in the landscape, these tree species offered a wide view of the surrounding area.

Similarities among nest sites used by Red-tailed Hawks in widely different habitats and geographical areas suggest the use of similar nest-site selection criteria (Mosher et al., 1986). A survey of the literature reveals that Red-tailed Hawk nests in North America are associated with large trees, forest edges, open canopy structure, and steep slopes (e.g., Jackson 1891, Jessee 1901, Bent 1937, Orians and Kuhlman 1956, Mader 1978, Petersen 1979, Bednarz and Dinsmore 1982). Titus and Mosher (1981) found that most of these characteristics were significantly different from those expected if the nest site was selected randomly. These characteristics converge on two properties: they permit a bird at the nest to view a large portion of its breeding territory and permit the nest to be seen from a distance.

The pattern of nesting in open situations that offer a wide field of view from the nest has also been reported for other species of raptors (Newton 1979, Andrew and Mosher 1982, Gilmer and Stewart 1983, Green and Morrison 1983). Four explanations for this pattern have been proposed: (1) hawks need an open canopy to obtain unobstructed access to the nest (Orians and Kuhlman 1956, Mader 1978, Bednarz and Dinsmore 1982,

Andrew and Mosher 1983), (2) they need wide views to detect predators at a distance (Belyea 1976, Blair and Schitosky 1982), (3) they need wide views to detect territorial intruders by using the nest as a surveying platform (Newton 1979), and (4) they use the visible nest as a territorial marker (Newton 1979). To this list we add a fifth explanation: adult Red-tailed Hawks spend a large portion of the day perched within their territory and they may need nests that are visible from these perches to detect aerial and scansorial predators approaching the nest. In rain and cloud forests adult Red-tailed Hawks seemed to prefer perches that offered a simultaneous view of their territory and their nest (Santana and Temple, in press).

Red-tailed Hawks probably choose nest sites that offer a wide view of their territory for many reasons, but territory defense could play an important role. Red-tailed Hawks are known to spend much of their flying time performing territorial displays and scanning their territories from perches (Ballam 1984, Janes 1984, Soltz 1984); territorial combat has been reported to last almost entire days (Janes 1984).

Red-tailed Hawks do not seem to select any one species of tree for nesting, and they also use cliffs and artificial structures (Smith and Murphy 1973, Olendorff et al. 1980). Red-tailed Hawks in Puerto Rico nested close to human activity; one pair nested successfully in an urban setting. This might be due to the high human densities on the island (400 people/$km^2$) (Birdsey and Weaver 1982). Nest sites that were very close to human activity were usually inaccessible to humans due to some factor other than horizontal distance (e.g., the presence of a river, fence, cliff, or other obstacle).

Red-tailed Hawks were not rare in Puerto Rico at the beginning of this century (Wetmore 1927, Danforth 1931), but their populations have apparently increased since the 1940s as agricultural lands and pastures reverted back to forest (Perez Rivera and Cotte Santana 1977, F. H. Wadsworth, pers. comm.). This land-use trend is no longer apparent, and during our study hunting, and nesting habitat were reduced in our lowland study areas as a result of development and urbanization. Unlike resident Broad-winged Hawks (*Buteo platypterus*) and Sharp-shinned Hawks (*Accipiter striatus*), which are uncommon in Puerto Rico due to their apparent need for large expanses of forest (Raffaele 1983), the wide habitat tolerances of Red-tailed Hawks have permitted them to remain common throughout the island. Increased habitat destruction, however, especially in lowland areas, will reduce nesting habitat for Red-tailed Hawks.

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# THE COURTSHIP BEHAVIOR AND MIXED-SPECIES PAIRING OF KING AND IMPERIAL BLUE-EYED SHAGS (*PHALACROCORAX ALBIVENTER* AND *P. ATRICEPS*)

DOUGLAS SIEGEL-CAUSEY[1]

ABSTRACT.—I compared the courtship behavior of King and Imperial Blue-eyed shags (*Phalacrocorax albiventer* and *P. atriceps*) for similarity and assessed their potential as a behavioral isolating mechanism between the two species. I could detect no differences in form or sequence of behavioral patterns, although there were some minor distinctions between forms. Observations were made near the end of the breeding season and may represent only the postbreeding behavior. I describe several new displays for King and Imperial shags, and contrast them with those known for the closely-related Antarctic Blue-eyed Shags (*P. atriceps bransfieldensis*). The courtship behavior of mixed-species pairs was nearly identical to conspecific pairs, and was difficult to distinguish. The observations do not support the existence of behavioral isolation between King and Imperial shags, but do support the contention that King Shags in Patagonia are color morphs of Imperial Blue-eyed Shags. *Received 15 Apr. 1986, accepted 10 July 1986.*

The specific status of the King Shag (*Phalacrocorax albiventer*) and its relationship with the Imperial Blue-eyed Shag (*P. atriceps*) is not well understood (Williams and Burger 1979, Brothers 1985). These two southern hemisphere cormorants are quite similar in appearance, differing only in external characters by plumage patterns of the cheeks and dorsum (Murphy 1936, Hellmayr and Conover 1948, Watson 1975). Both species breed along the Fuego-Patagonian coast, frequently within the same colony (Behn et al. 1955, Devillers and Terschuren 1978). Devillers and Terschuren concluded after extensive field observations that between 15% and 20% of the members of sympatric populations were intermediate in plumage characters, that mixed-species pairs exist, and that the King Shag should, at best, be considered as a subspecies of the Imperial Blue-eyed Shag. Much of their evidence, however, relied exclusively upon photographs and field observations of crowded colonies where juveniles and prebreeding adults could be confused with mated pairs. Rasmussen (1986) reported that Imperial Shags in juvenal plumage often superficially resemble King Shags, and such photographs may possibly represent experimental pairings between adults and juveniles, events that occur occa-

[1] Museum of Natural History and Dept. Systematics and Ecology, Univ. Kansas, Lawrence, Kansas 66045.

sionally in cormorant colonies during the latter half of the nesting season (Lewis 1929).

One approach to elucidating this problem is to examine the courtship behavior of each species, and investigate in more detail the circumstances of mixed-species pairs. If these two forms are distinct species, there should be behavioral isolating mechanisms in zones of sympatry (see Bernstein and Gordon 1979). Here, I compare the courtship behavior of conspecific and heterospecific pairs of King and Imperial Blue-eyed shags and test for similarity.

## METHODS

In late January 1985, I observed a colony of about 55 pairs of King Shags on Isla Escobar near Puerto Melo, Provincia de Chubut, Argentina (see Livezey et al. 1985 for a description of the area). During February 1985, I observed both King and Imperial shags at a staging area on Roca Foca and Isla de Cañadon del Puerto near Puerto Deseado, Provincia de Santa Cruz, Argentina (see Zapata 1967 for details). Both species breed on nearby Isla Chata, Bahia Oso Marino, in a colony estimated at 5000–10,000 nests, 80% of which were Imperial Blue-eyed Shags; the remainder were King Shags (Devillers and Terschuren 1978). I used 7 × 50 binoculars and a 45× telescope to observe courting pairs. I recorded behavioral acts in shorthand and on 35 mm slide film. I sexed birds by relative bill size and behavior (see Bernstein and Maxson 1982). Observation periods ranged from 1 to 5 h; the total amount of time spent observing behavior was equivalent to about 9000 bird-h. When I began, breeding was still underway, but all of these observations were made late in the breeding season. Thus, the courtship behavior I observed may not represent the full range associated with pairs mating earlier in the season.

As the ancestry of hybrids was unknown, I used only courtship sequences from conspecific and heterospecific pairs of King and Imperial Blue-eyed shags. Display terminology follows van Tets (1965) except where noted. Bernstein and Maxson (1982) described the behavior and habits of a closely related form, the Antarctic Blue-eyed Shag (*P. atriceps bransfieldensis*). I have relied upon their descriptions where possible and discuss only those displays not described there.

## BEHAVIOR

*Take-off from land.*—Departure from the nest or colony has the potential for disturbing neighbors and alarming the remaining mate and chicks. To reduce these problems, most cormorants use a ritualized display of three phases: Look, Crouch, and Leap (van Tets 1965). Bernstein and Maxson (1982) were unable to see the Crouch phase in Antarctic Blue-eyed Shags, but both King and Imperial shags I watched always employed a distinct Crouch before the Leap. In this phase the breast is dropped and the wings are partly opened; the Look and Leap phases do not differ substantially from that of other cormorants (see fig. 7 in van Tets 1965).

*Hop.*—This display is distinguished from normal locomotion by its ritualized slowness and in that the head and neck are pointed down toward the feet (see Fig. 10 in van Tets 1965). Although I observed this display

in both King and Imperial shags, Bernstein and Maxson (1982) did not observe it in the Antarctic Blue-eyed Shag.

*Kink-throating.*—This distinctive display is used by many cormorant species before landing. The hyoid is depressed forward, greatly enlarging the gular pouch, and is often accompanied by slight lateral headwaving (see Fig. 37 in van Tets 1965). Expansion of the gular pouch by the hyoid occurs in many contexts (during courtship, before take-off, in pair-recognition, etc.), and may not always be a distinct display. Instead, it may be employed as a behavioral adjunct by enabling the yellow gular pouch to be displayed as a visual signal. Both species always employed it when approaching their nests and about 60% of the time when landing near small groups of congeners. I saw it only about 10% of the time when the shags landed alone. Bernstein and Maxson (1982) did not see Kink-throating used during landing by the Antarctic Blue-eyed Shag, but this may have been a result of observational problems they encountered (Bernstein, pers. comm.). I was unable to detect any difference between King and Imperial shags in their use of Kink-throating before landing or during courtship.

*Threatening.*—King and Imperial shags used several displays in defense of their nest and its contents. When intruders were farthest from the nest, the most common display used was Snaking, a characteristic display of cormorants where the gaping bill is waved deliberately, often with the neck fully extended (Siegel-Causey 1978). When intruders came closer or were not deterred by Snaking, they used Thrusting (Siegel-Causey 1978), a rarer display. In this display, the head and neck are quickly extended at the intruder with the bill gaped and then retracted backwards. This threat was often repeated quickly 5–6 times by the defenders before subsiding into Snaking or motionless staring. Another display, Nest-indication, was given along with Snaking and Thrusting, possibly as redirected aggression. Bernstein and Maxson (1982) observed only Snaking in the Antarctic Blue-eyed Shag and did not see Nest-indication used during threats or fighting. Most other species of cormorants studied (van Tets 1965, Berry 1976, Siegel-Causey 1978) apparently use Nest-indication as a mild threat and to indicate site ownership. I detected no differences in threat behavior between King and Imperial shags off the breeding colony; I did not collect sufficient data for comparisons of defense behavior by either shag when in the breeding colony.

*Male advertising.*—Bernstein and Maxson (1982) described the male advertising display, Gargling, of Antarctic Blue-eyed Shags. The only difference I observed in King and Imperial Blue-eyed shags was that they rolled their head once from side-to-side at full Throwback position in 69% of the observations. Antarctic Blue-eyed Shags only occasionally did this (Bernstein, pers. comm.). This appears to be similar to what is de-

scribed as Gaping in the Great Cormorant (*P. carbo*) (see Fig. 26 in van Tets 1965), which is a bisexual recognition display. I never observed this movement in female King or Imperial shags, and males employed it only in conjunction with Gargling. Because of this high association with Gargling, I doubt that it constitutes a distinct display in either species. King Shags seemed to Gape more often (71% of observations) than Imperial Shags (56%) when at full Throwback, but I saw no differences in form between the species.

*Recognition and pairbonding.*—King and Imperial Blue-eyed shags use various displays in recognition and pairbonding. Throat-clicking (Snow 1963, fig. 3b in Bernstein and Maxson 1982) was employed in many circumstances ranging from nest relief to maintenance of the pairbond. Although Bernstein and Maxson (1982) assigned different roles to each sex in Throat-clicking in the Antarctic Blue-eyed Shag, I saw no sexual differences in performance for either King or Imperial shags, nor could I see any differences in form between species.

A movement similar to Throat-clicking was employed only in courtship, usually preceding and following copulation. The female faced the male (unlike in Throat-clicking where the pair is side-by-side), repeatedly nibbled or bit the tip of the male's bill ("Bill-biting"), and waved her open beak. The male responded by remaining motionless or initiating another pairing display such as Allopreening or Head-wagging (see fig. 3a in Bernstein and Maxson 1982).

*Pointing and Darting.*—Although Bernstein and Maxson (1982) never observed these displays in the Antarctic Blue-eyed Shag, pointing and darting were among the most common recognition displays employed by King and Imperial Blue-eyed shags. In Pointing, the neck, head, and closed bill were stretched forward and upward, with neck and head feathers erected (see fig. 29 in van Tets 1965). In the context of a recognition display, it always was done very deliberately by either sex on the nest. It was held for 1–2 sec, and was followed by Nest-indication. In other cases, it was combined with Darting as a courting display, usually by the male standing or slightly crouching. I saw no intra- or interspecific differences in Pointing.

Both shags Darted by retracting their head and folding their neck medially over the back with their bill kept forwards. The bill was then moved from side-to-side. This display was repeated rapidly 2–5 times and then the cycle of Pointing-Darting started again. After 3–4 cycles, the male terminated the action with a modified Pointing display which differed by the mandible moved to curve upwards at the tip, held for about 2 sec. King and Imperial Blue-eyed shags performed the display similarly, differing only in the number of cycles (Kolmogorov-Smirnov Two-sample test, $D = 0.57$, $P < 0.01$) (Table 1).

TABLE 1
DURATION IN CYCLES OF THE POINTING/DARTING DISPLAY BY MALE IMPERIAL AND KING SHAGS[a]

| Number of cycles | Imperial Shag | King Shag |
|---|---|---|
| 1 | 0 | 3 |
| 2 | 1 | 5 |
| 3 | 5 | 14 |
| 4 | 12 | 2 |
| 5 | 6 | 2 |
| 6 | 1 | 1 |
| 7 | 5 | 1 |

[a] Only displays that were followed by the arrival of a female were counted.

The male, if alone, self-preened after Pointing-Darting in 86% of the observations, most often at the white alar bar or breast feathers. If done with a partner, mutual Allopreening, directed mostly towards the sides of the neck, occurred 95% of the time. I saw no difference between King and Imperial shags in self-preening behavior (Kolmogorov-Smirnov Two-sample test, $P > 0.10$) (Table 2) or Allopreening ($P > 0.10$) (Table 3). That males tended to preen their white alar bars after displaying strongly suggests a signal value for this display. It may have been derived from simple allopreening (both sexes preen their white alar bars), and later used for initiating and maintaining the pairbond.

## MIXED-SPECIES PAIRS AND COURTSHIP SEQUENCES

Devillers and Terschuren (1978) reported a small number of mixed-species pairs allopreening and guarding nests and chicks at sites along the

TABLE 2
PRIMARY SITES OF SELF-PREENING AT THE CONCLUSION OF THE POINTING/DARTING DISPLAY BY MALE IMPERIAL AND KING SHAGS[a]

| Preening site | Imperial Shag | King Shag |
|---|---|---|
| Neck | 2 | 3 |
| Breast | 4 | 2 |
| Abdomen | 0 | 1 |
| Upper wing | 2 | 1 |
| Alar bar | 17 | 21 |
| Back | 1 | 0 |
| Crissum | 1 | 1 |

[a] A primary site was the first body area continuously preened after the display.

TABLE 3

PRIMARY SITES OF ALLOPREENING AT THE CONCLUSION OF THE POINTING-DARTING DISPLAY BY IMPERIAL AND KING SHAGS[a]

| Preening site | Pairing[b] | | | |
|---|---|---|---|---|
| | Imperial × Imperial ($N$ = 30) | King × King ($N$ = 33) | Imperial × King ($N$ = 7) | King × Imperial ($N$ = 23) |
| Neck | 11 | 13 | 4 | 10 |
| Breast | 7 | 5 | 1 | 5 |
| Abdomen | 0 | 1 | 0 | 0 |
| Upper wing | 2 | 1 | 0 | 1 |
| Alar bar | 8 | 11 | 2 | 9 |
| Back | 1 | 1 | 0 | 1 |
| Crissum | 1 | 1 | 0 | 3 |

[a] A primary site was the first body area continuously preened by the male after the display.
[b] The first species in the pairing caption represents the male.

Fuego-Patagonian coastline. At various sites on or near Puerto Deseado used by courting King and Imperial Blue-eyed shags from the nearby breeding colony on Isla Chata (see Devillers and Terschuren 1978 for details of the colony), mixed-species pairs constituted about 8% of the 451 pairs observed. Male King and female Imperial courting pairs comprised two-thirds (N = 23) of these pairs. I saw no differences in the forms of courtship and recognition displays among any of the conspecific and heterospecific pairings. If a behavioral isolating mechanism does exist, it must instead be a difference in courtship sequence, rather than one involving different displays.

To examine the courtship sequences of each class of pairings, I accumulated male-to-female and female-to-male behavioral dyads for each courtship sequence that ended in mounting. I constructed contingency tables using the dyadic frequencies, and from them constructed conditional probabilities of the various male–female and female–male transitions. Transitions occurring most frequently in each pairing are in Fig. 1. Because of small sample sizes and the unknown applicability to courtship patterns used early in the breeding season, I was unable to test for higher-order patterns or gender differences.

There are no differences among courtship sequences used by hetero- and conspecific pairs of King and Imperial Blue-eyed shags (Hilton's G test: 1a–1b, $P > 0.20$; 1a–1c, $P > 0.10$; 1a–1d, $P > 0.10$; 1b–1c, $P > 0.10$; 1b–1d, $P > 0.25$; 1c–1d, $P > 0.10$) (Fig. 1). There were some qualitative distinctions between conspecific pairs of King and Imperial Blue-eyed shags: King Shag males often initiated Head-wagging after a female began Throat-clicking (Fig. 1a), and Imperial Blue-eyed Shag females

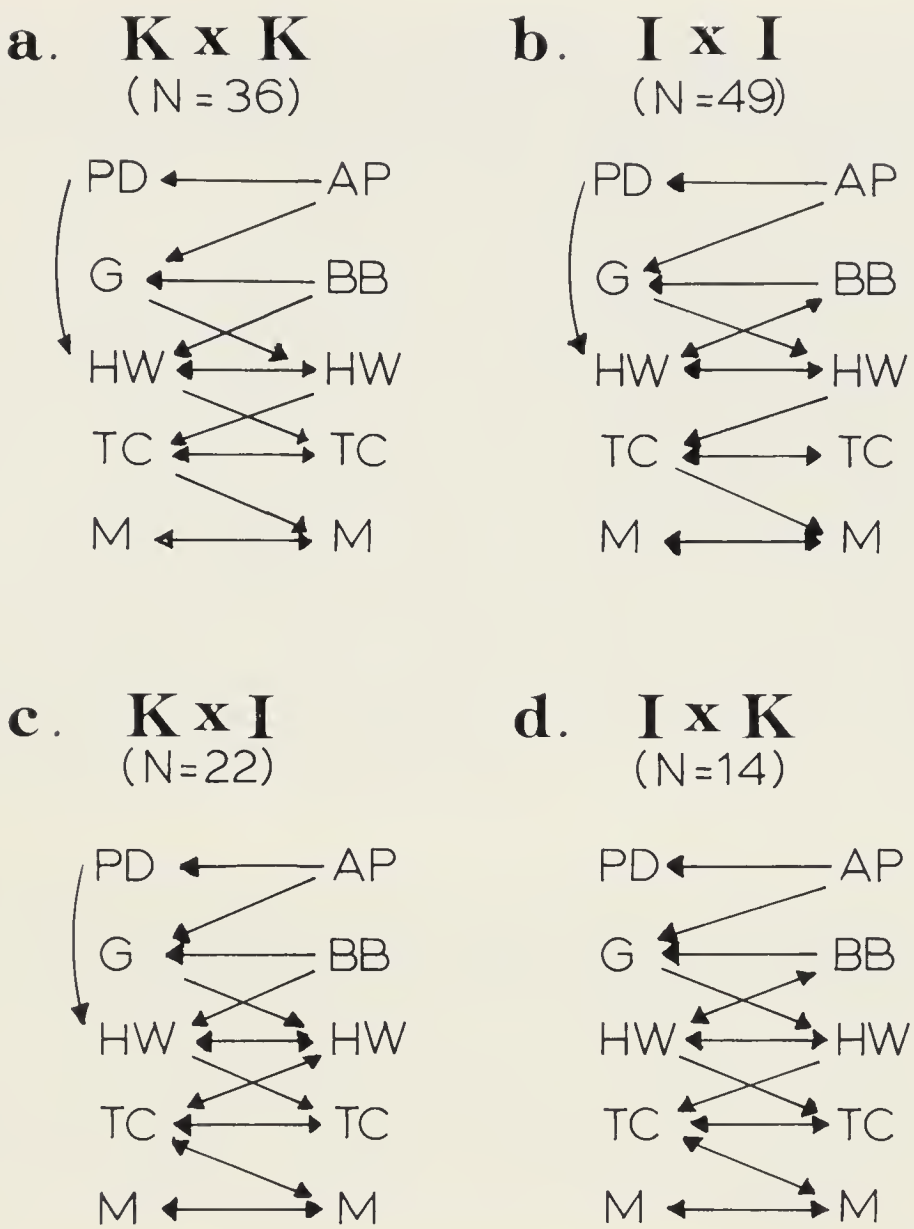


FIG. 1. Sequence diagrams for the courtship behavior of King and Imperial Blue-eyed shags. Sequence captions are male species × female species: (a) King × King, (b) Imperial × Imperial, (c) King × Imperial, (d) Imperial × King. Sample sizes are given in parentheses. Behavior sequences for each sex run from top to bottom in each column; interaction directions are indicated by arrows. AP: Approach and head alignment; BB: Bill-biting; G: Gargling; HW: Head-wagging; M: Mounting; PD: Pointing-Darting; TC: Throat-clicking.

often continued Bill-biting after males initiated Head-wagging (Fig. 1b). Mixed-species pairs showed the influence of both partners, and the only distinction observed was that male Imperial Shags always preceded Gargling with the Pointing-Darting display (Fig. 1d). In contrast, male King Shags frequently skipped Gargling and went straight to Head-wagging (Fig. 1c). None of these differences, however, was significant.

## DISCUSSION

In addition to my inability to find differences in form or sequence of courtship displays, the courtship sequences employed by heterospecific pairs were generally indistinguishable from those seen in conspecific pairings. Allopreening between different species has not been reported in the Phalacrocoracidae prior to Devillers and Terschuren's (1978) investigation, and hybrids in the family are rare. It appears that for King and Imperial Blue-eyed shags, the behavioral barriers to introgression are weak or nonexistent. If assortative mating occurs, it must be accomplished by other means, perhaps through morphological differentiation or allopatry.

In the Emperor Shag (*P. albiventer purpurascens*), pairbonds frequently were broken between and among seasons, and mate retention did not seem to be influenced by reproductive success (Brothers 1985). Antarctic Blue-eyed Shags show a similar rate of mate change (Bernstein and Maxson 1982), unrelated by age of partner, prior or subsequent breeding success (Shaw, in press). This low mate fidelity could allow greater latitude in mate choice, and serve to maintain the presence of mixed-species pairs. Devillers and Terschuren (1978) found heterospecific pairs at each sympatric colony they visited.

Some of the King and Imperial Blue-eyed shags I observed may represent immature birds practicing courtship or attempting maladaptive pairings. Although Rasmussen (1986) reported similarities in cheek patch patterns between juvenile Imperial Shags and adult King Shags, confusion between the two seems unlikely except at a distance. The overall appearance of first-year birds is very different from that of their elders (Shaw, pers. comm.) in coloration of the gular pouch, development and coloration of caruncles, and absence of nuptial plumage and filoplumes (see Derenne et al. 1976). Furthermore, early breeding in King and Imperial shags is uncommon.

Emperor Shags on Macquarie Island generally breed by their fourth year, although a few attempt breeding as soon as they attain adult plumage at 2 years of age (Brothers 1985). Antarctic Blue-eyed Shags on the South Orkney Islands were able to raise successful broods at 3 years of age, but the mean age of pairs was higher, about 6.5 years (Shaw 1985b). The youngest birds were mostly paired with older mates, only equaling or exceeding their age by age five (females) or age seven (males) (see fig. 2 in Shaw 1985b). Birds less than 7 years of age arrived at the colony significantly later than older birds, and younger pairs nested generally on the periphery with a lower reproductive success (Shaw 1985a). Juvenile or inexperienced birds may comprise one or both courting partners of a mixed pair; assortative pairing may become more common with the mean age of the pair as morphological discrimination develops. If this is the

case, then mixed pairings should occur only in pairs involving younger birds. Similar demographics may contribute to the scarcity of mixed-species pairs along the Fuego-Patagonian coast and the absence of strong behavioral isolating mechanisms between King and Imperial Blue-eyed shags.

The differences in courtship and pairbonding behavior of King and Imperial Blue-eyed shags compared with Antarctic Blue-eyed Shags are difficult to explain. Although my investigation was based only on observations of adults in breeding plumage, about half represent pairs off the breeding colony near the end of the breeding season (February). Nonetheless, these sequences did not deviate significantly from those seen on the breeding colony on Isla Escobar earlier in the season. These differences, if not artifacts of observational error, indicate that the relationship between King and Imperial Blue-eyed shags may be closer than currently postulated between Imperial and Antarctic Blue-eyed shags. In that case, King and Imperial Blue-eyed shags should probably be considered, as suggested by Devillers and Terschuren, as subspecies or color morphs of a single species, *Phalacrocorax atriceps.*

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# GENERAL NOTES

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**Dispersal of recently fledged Mourning Doves from nest sites.**—Reports of fledgling Mourning Dove (*Zenaida macroura*) movements have been vague and variable because of difficulty following unmarked birds (e.g., Mackey 1954). Other studies using marked Mourning Doves did not investigate the relationship between dispersal and fledgling age (e.g., Tomlinson et al. 1960). Our research has focused on behavioral interactions between fledgling Mourning Doves and their parents (Hitchcock and Mirarchi 1984a, b, 1985). Herein, we report on dispersal of juvenile Mourning Doves from nest sites.

*Methods.*—We located Mourning Dove nests in east-central Alabama from March through September 1980–81. Nestlings were aged by daily growth stages (Hanson and Kossack 1963). The oldest nestling of 35 normal broods was fitted with a radio transmitter at 7–8 days of age (Hitchcock and Mirarchi 1984a). Movement data were collected from only 24 of these nestlings due to nestling mortality prior to fledging. Nestlings usually fledged at 15 days of age.

We observed radio-tagged doves during 3 daily periods (period 1, 15 min before to 2 h after sunrise; period 2, 12:00–14:00 h; and period 3, 2 h before to 15 min after sunset) when fledglings were 15–21, 24, 27, and 30 days of age. We observed fledglings at distances (30–60 m) that did not appear to interfere with their normal behavior. We also observed them on the roost at least ½ h after dark on each observation day using a 200,000 candlepower spotlight.

We recorded the initial, final, and maximum distance from the location of the fledglings back to the trunk of the nest tree during each daytime observation period and calculated the maximum distance that fledglings were found from the nest tree on any given day from these data. Three or more daily locations of a fledgling were required to establish this value. We also recorded distances from roost sites to nest trees. Locations where fledglings were found for 3 or more observation periods (consecutive or otherwise), and which were used

TABLE 1

DISTANCES ($\bar{x} \pm$ SE) BETWEEN FLEDGLING MOURNING DOVE REFERENCE AREAS AND NEST TREES RELATIVE TO AGE, EAST-CENTRAL ALABAMA, 1980–81

| Age (days) | *N* | Distance (m) |
|---|---|---|
| 15 | 22 | $6 \pm 3^{a}$ |
| 16 | 23 | $11 \pm 3^{ab}$ |
| 17 | 23 | $16 \pm 3^{ab}$ |
| 18 | 23 | $20 \pm 3^{bc}$ |
| 19 | 22 | $21 \pm 3^{bc}$ |
| 20 | 22 | $23 \pm 3^{bc}$ |
| 21 | 22 | $28 \pm 3^{cd}$ |
| 24 | 20 | $39 \pm 3^{d}$ |
| 27 | 15 | $41 \pm 4^{d}$ |

[abcd] Column means not having a common superscript are different (Tukey test, $\alpha = 0.05$).

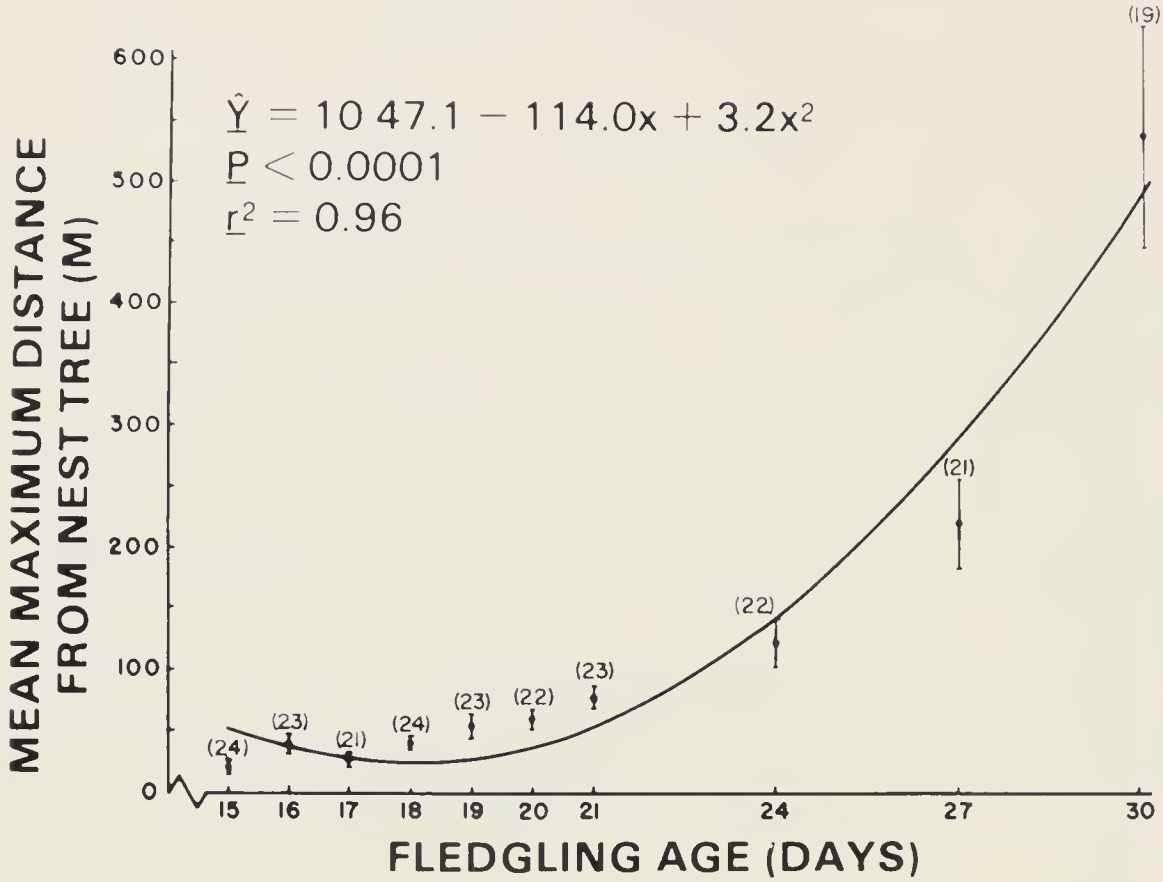


FIG. 1. Regression (calculated from means) of the maximum distance fledglings moved from nest trees. Numbers in parentheses represent number of fledglings sampled.

for interactions with parents, were designated as reference areas. We averaged distances from the nest tree to reference areas by age for each fledgling. Distances of less than 250 m were measured by pacing. Longer distances were measured using 61 × 61-cm (linear scale 2.5 cm = 201.2 m) aerial photographs. We used only the central areas of the photographs to ensure accuracy of measurements.

We tested the maximum distance in each daily time period against daily time period and age, and distances to reference areas against age using 2 and 1 factor within-subject designs, respectively (Keppel 1982). In both analyses, 30-day-old birds were eliminated because they were no longer centering their activities around former nest trees. Pairwise comparisons between means were obtained using Tukey's test (Familywise error rate = 0.05; Keppel 1982). Separate quadratic regressions were calculated from the means for maximum distance moved each day and distance to the roost sites, and were analyzed by fledgling age (Neter and Wasserman 1974). Because we used mean values, coefficients of determination do not reflect the relatively high variation associated with the movements of individual birds.

*Results and discussion.*—Fledglings generally loafed in reference areas within 45 m of the nest tree through 27 days posthatching (PH) where they were fed frequently by the male parent (Table 1). These findings are similar to those of other studies on fledgling Mourning Doves (Moore and Pearson 1941, Webb 1950, Mackey 1954, Morrison 1969), Wood Pigeons (*Columba palumbus*) (Murton 1965), White-winged Doves (*Zenaida asiatica*) (Cottam and Trefethen 1968), and White-crowned Pigeons (*Columba leucocephala*) (Wiley and Wiley 1979). Fledglings used more than one reference area ($\bar{x}$ = 3.1) during the dependency period.

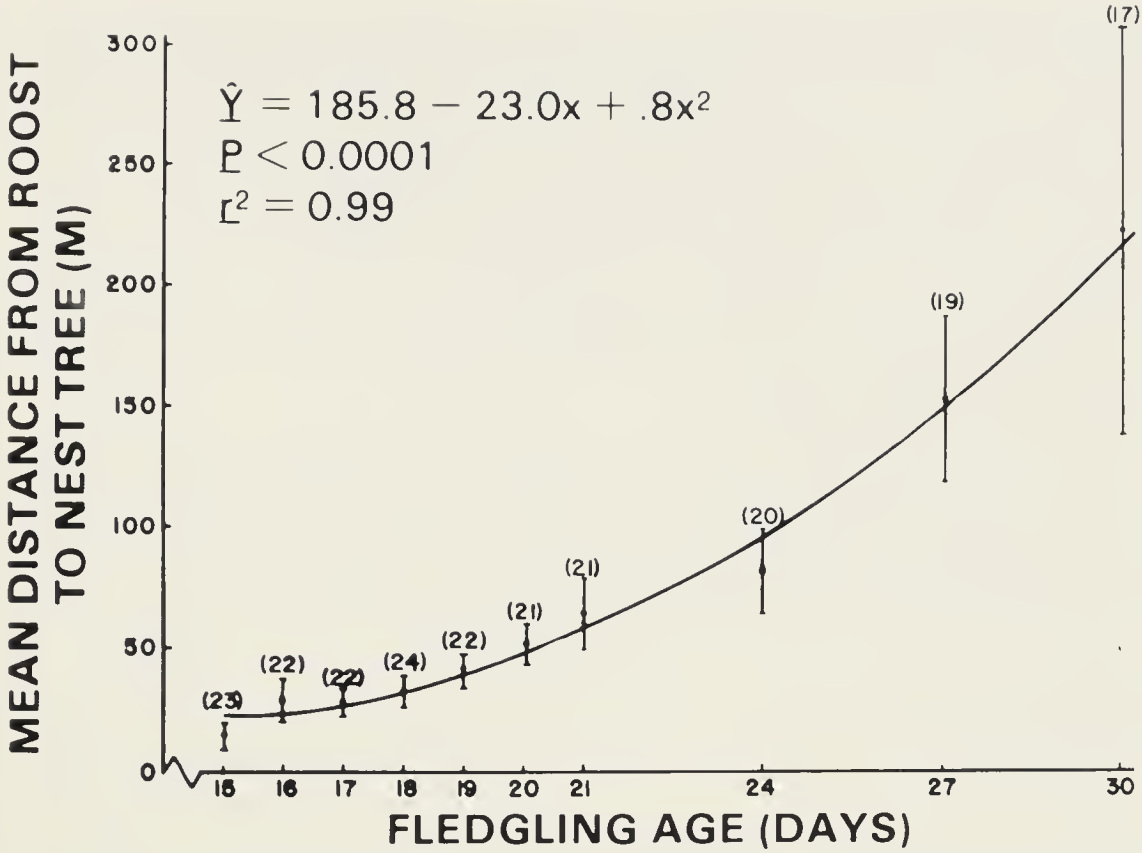


FIG. 2. Regression (calculated from means) of distance fledglings moved between nest sites and roost trees. Numbers in parentheses represent number of fledglings sampled.

Reference areas (approx. 3 $m^2$) were in trees (often on particular limbs) and on the ground and were characterized by dense overhead cover interspersed with openings that facilitated parent-young feeding interactions (Grand 1984). Fledglings used reference areas farther from the nest tree as they grew older (Table 1), and at 24 and 27 days of age they loafed farther from the nest tree ($P < 0.05$) than did 15–20-day-old young. As the older fledglings became self sufficient (Hitchcock and Mirarchi 1984a) they moved among different openings on the ground and often established new reference areas.

The maximum distance moved each day increased with age, the rate of increase being greatest after 21 days PH (Fig. 1). This probably reflects completion of feather development at 20 to 21 days of age (Moore 1940), which results in a noticeable improvement in flight. The maximum distance moved by fledglings ≤21 days old was 257 m, but at this age fledglings rarely moved more than 70 m from the old nest site except when disturbed. Movements of >70 m were achieved by several short flights. Fledglings driven from reference areas by predators or human disturbance, and who were still dependent on parental care, always returned to those areas within 24 hours.

By 21 to 24 days of age some fledglings moved from their reference areas and centered their daily activities around abundant food supplies (Hitchcock and Mirarchi 1984a). The maximum distance moved by fledglings at this age was 345 m, and such fledglings generally were unable to fly with older juveniles in flocks. Fledglings moved greater distances at 27 and 30 days of age, usually in association with flocks of juveniles flying to feeding sites. Maturation of flight capabilities, greater sociability, and declining parental care contributed to increased fledgling mobility at this age (Hitchcock and Mirarchi 1984a).

Distances moved from nest trees to roost sites increased steadily with age (Fig. 2). During the period of fledgling dependency (ages 15–27 days) the maximum distance moved each day was usually to the roost site (61% of 199 observations). Roost sites often provide protection from predators (Pettingill 1970). The low frequency of use of the same roost site by fledglings that were dependent upon parental care may be an adaptation to prevent nocturnal predators from locating areas consistently used for roosting and may explain the relatively great distances flown by such fledglings each evening (Grand 1984).

Fledglings were found farther from nest trees during observation periods 1 (56 ± 4 m [SE]) and 3 (65 ± 4 m) than during period 2 (36 ± 4 m; $P = 0.05$) because of longer movement to and from roosts as well as general activity patterns during the morning and evening hours. Fledglings were most active at times previously reported for adult Mourning Doves (Duever and Fatora 1968).

This study indicates that Mourning Dove fledglings generally loaf in reference areas within 45 m of former nest sites through 27 days of age. However, development of flight capabilities and increasing ability to forage independently allows fledglings >21 days of age to establish new reference areas farther from the nest site and to travel greater distances to feed when necessary. Generally, fledglings do not abandon reference areas until they are 27 to 30 days old, at which time they are mobile enough to join juvenile flocks that may travel up to 1500 m from the nest site. During the period of fledgling dependency, maximum distances moved each day are usually to roost sites which are changed frequently, possibly to avoid nocturnal predators.

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RONALD R. HITCHCOCK AND RALPH E. MIRARCHI, *Dept. Zoology and Wildlife Science, and Alabama Agricultural Experiment Station, Auburn Univ., Auburn, Alabama 36849-4201.*
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**Observations on the breeding biology of Emerald Toucanets in Costa Rica.**—Emerald Toucanets (*Aulacorhynchus prasinus*) are abundant in montane forests of Central America, but their breeding biology has received little study (Wagner 1944; Skutch 1944, 1967). Here I provide data on the roles of sexes in parental care of young Emerald Toucanets and describe nestling diet.

*Study area and methods.*—The study was conducted in and around Monteverde, Costa Rica (10°18′N, 84°48′W) in scattered cattle pastures and small- to moderate-sized woodlots in montane wet forest. For a more detailed description of the area, see Lawton and Dryer (1980) and Holdridge (1967).

Observations were made during July–August 1984 and March–July 1985. Nests were monitored daily for 1–2 h (alternating mornings and afternoons) with 8 × 35 binoculars for a total of 107 h by me and 5 assistants. During each visit, percent time each sex spent in each activity (e.g., excavation, incubation, waste removal) was calculated. Based on a morphometric analysis of museum specimens (Riley 1986), I could reliably sex most toucanets in the field. Food items delivered to nestlings were classified as either insect or fruit, and more accurate identifications were made when possible. I calculated percent fruit in the nestling diet as well as percent of nests that fledged at least one chick.

*Results.*—Courtship feeding was first observed in mid-March. I saw males, perched next to a female, offer fruit on 3 occasions. Acceptance of the fruit was followed by copulation in 2 cases. Nest excavation began within a few days of courtship. A total of 13 nests was found, 3 in 1984 and 10 in 1985. All nests were in pastures or forest edges in old snags, except for one in a wooden utility pole along a roadcut. Nests were either enlarged wood-

TABLE 1

MORPHOMETRICS OF FRUITS BROUGHT TO NESTLING EMERALD TOUCANETS DURING 1984 AND 1985 (AS SOME FRUITS WERE NOT REPORTED TO SPECIES LEVEL, THIS LIST MAY UNDERESTIMATE THE DIVERSITY OF FRUITS IN NESTLING DIETS)

| Fruit | Mean | | |
|---|---|---|---|
| | Length (mm) | Width (mm) | Weight (g) |
| *Ocotea tonduzii* | 15.3 | 10.1 | 1.0 |
| *O. tenera* | 25.4 | 17.7 | 6.3 |
| *Trema micrantha* | 3.1 | 2.5 | 0.02 |
| *Cecropia* spp. | 44.9 | 6.9 | 1.9 |
| *Hasseltia floribunda* | 11.2 | 10.8 | 0.8 |
| *Passiflora helleri* | 16.8 | 17.0 | 3.0 |
| *Rapanea myricoides* | 0.4 | 0.4 | 0.03 |
| *Ehretia austin-smithii* | 15.7 | 14.2 | 2.1 |
| *Acnistus arborescens* | 7.7 | 8.3 | 0.3 |
| *Cestrum* spp. | 9.5 | 7.8 | 0.3 |
| *Lycianthes multiflora* | 11.8 | 12.3 | 1.0 |
| *Citharexylum macradenium* | 9.9 | 9.9 | 0.8 |
| *Rubus rosaefolia* | 13.7 | 13.5 | 1.4 |
| *Conostegia bernouliana* | 7.4 | 10.1 | 0.5 |
| *Dendropanax* spp. | 7.6 | 9.3 | 0.3 |
| *Oreopanax* spp. | 4.0 | 4.0 | 0.05 |
| All species | 12.8 | 9.7 | 1.2 |

pecker holes (Skutch 1944) or excavations in rotten trees. Nest height varied from 3.2 to 7.4 m ($\bar{x}$ = 5.4 m, N = 3). Hole openings were oval shaped and averaged 7.3 cm wide, 7.7 cm long and 57 cm deep (cf. Skutch 1944). I observed excavation activity for 2 h at 2 nest sites. Females were responsible for 58% of the excavation. Once excavation was complete, 3–5 eggs were laid directly on the wooden floor of the cavity.

I observed incubation activity for 7.8 h at 2 nests in 1985. The first nest was monitored for 7 days in late May, after which it was destroyed by White-faced Monkeys (*Cebus capucinus*) (B. Haber, pers. comm.). The second nest (with 3 eggs) was watched for 2 days in late June prior to being lost to predation. During these brief observations, both adults incubated for short periods (females $\bar{x}$ = 15.5 min, N = 15; males $\bar{x}$ = 11 min, N = 20), with females incubating 66% of the time. Although I did not follow the entire cycle of any one nest, Skutch (1967) found the incubation period to be 16 days.

*Nestling diet.*—Fruits, arthropods, and a bird's egg (delivered by a male) were brought to >30-day-old nestlings at 6 nests. Nestlings fledged at 5 of these sites. Percent fruit delivered to nestlings at those 5 sites ranged from 85 to 97%. The remainder of nestling diets were arthropods. At the remaining site, I observed food deliveries for 12 of the first 15 days after hatching. Nestling diet consisted of 67% fruit for the 12 observation days (13 h, N = 88 deliveries).

Adults of both sexes fed at similar rates (females, $\bar{x}$ = 2.48 ± 0.53 deliveries/h, N = 244 food items; males, $\bar{x}$ = 2.88 ± 0.59, N = 296 food items), but males fed insects more frequently (0.67 insects/h, N = 76) than did females (0.36 insects/h, N = 36). Sixteen species

of fruit (Table 1) comprised 79% of 539 food items delivered. All species of fruits delivered to young were also common in the diets of adults. Arthropods (21% of food items) included a spider (Arachnida), 2 centipedes (Diplopoda), Orthoptera (Phasmatidae [12], Gryllidae [1], Tettigoniidae [2]), Homoptera (1), Coleoptera (14), Lepidoptera (6), Diptera (11), and Hymenoptera (1). The remaining 64 arthropods could not be identified.

*Nest sanitation.*—The adults removed wood chips following excavation and carried nestling fecal sacs and regurgitated seeds from the sites. Females performed 78% of the 167 waste removal acts I observed at 9 nests.

*Nesting success.*—I was able to determine the outcome of 10 of the 13 nesting attempts I watched. Six fledged at least one chick (3 clutches of 4, 1 clutch of 3, 1 clutch of 1). Two nesting attempts were second clutches fledging 1 and 4 chicks. At the sixth nest I saw young with adults, but was unable to determine the exact number fledged. Two nests failed to fledge young due to treefalls, 2 nests failed due to predation, and one nest was abandoned before excavation was complete. The outcome of 2 nesting attempts was unknown.

*Discussion.*—Skutch (1944, 1967) reported findings for 11 nests in Costa Rica, all of which were in pasture clearings, 2.1–27.4 m high in woodpecker cavities. Most nests contained 3 or 4 eggs that were incubated equally by both adults for 16 days; although others had slightly longer incubation sessions and more male incubation. Young fledged at 43 days of age, and second broods were common.

Skutch (1944) and Wagner (1944), who observed a single nest of an Emerald Toucanet in Chiapas, Mexico, also observed that nestlings were fed a diet consisting mainly of fruits and only a few insects. Skutch (1967) observed toucanets occasionally feed eggs and nestlings of other birds to young.

Most tropical fruit-eating birds feed their nestlings much greater proportions of animal material (Snow 1976) than that found for toucanets. Wheelwright (1983) found that nestling Resplendent Quetzals (*Pharomachrus mocinno*), another hole-nesting species at Monteverde, received 70% animal food, although adults seldom eat anything but fruits. Lengthy development periods have been documented for several frugivorous species (Snow 1962). Morton (1973) suggested that nestling diets high in fruits are not favored for most birds because resultant slow growth would subject young to increased predation pressures. Emerald Toucanets and other ramphastids fledge at 35–43 days after hatching (Van Tyne 1929; Skutch 1944, 1945, 1967; Todd et al. 1973). Despite this long nestling period, Emerald Toucanets in my study were preyed on at only 2 of 10 nests. Toucanets may experience low rates of predation because of nest type and location, as well as their aggressive behavior toward intruders. Skutch (1966) found that nesting success was greatest in tropical species with deep hole nests in second growth habitats, the nesting pattern of Emerald Toucanets.

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CECILIA M. RILEY, *Dept. Zoology, Univ. Arkansas, Fayetteville, Arkansas 72701.* (Present address: *Univ. Texas Marine Science Institute, Port Aransas, Texas 78373.*) *Received 6 Dec. 1985, accepted 16 May 1986.*

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**Seabird densities and aggregations during the 1983 El Niño in the Galapagos Islands.**—The El Niño-Southern Oscillation (ENSO) phenomenon of 1982–1983 was one of the most severe ever recorded in the Pacific Ocean, with major changes in fisheries, climate, and bird populations (Barber and Chavez 1983). In the Galapagos Islands, approximately 1000 km off the west coast of South America, Valle (1985) documented major breeding population decreases of Flightless Cormorants (*Nannopterum harrisi*) and Galapagos Penguins (*Spheniscus mendiculus*) and observed mortality of Blue-footed Boobies (*Sula nebouxii*), Magnificent (*Fregata magnificens*) and Great (*F. minor*) frigatebirds, and Brown Pelicans (*Pelecanus occidentalis*). Effects appeared to be more severe than during previous occurrences of El Niño, when adult mortality was not reported (Boersma 1978, Harris 1979). The widespread adult mortality and reproductive failure reported for breeding seabirds (Valle 1985) most probably were caused by reductions in food resources in the marine environment (e.g., Boersma 1978) during the 1983 El Niño. Unfortunately, there has been little information on seabird distribution and numbers at sea during El Niño events in the Galapagos. We report seabird densities and flock sizes recorded on 6 transects made within the archipelago during and after the 1983 El Niño.

*Methods.*—Birds were counted on continuous transects between islands, using the vessel Beagle III, cruising at 8 knots (Fig. 1). Sea-surface temperatures (SST) were taken with bucket

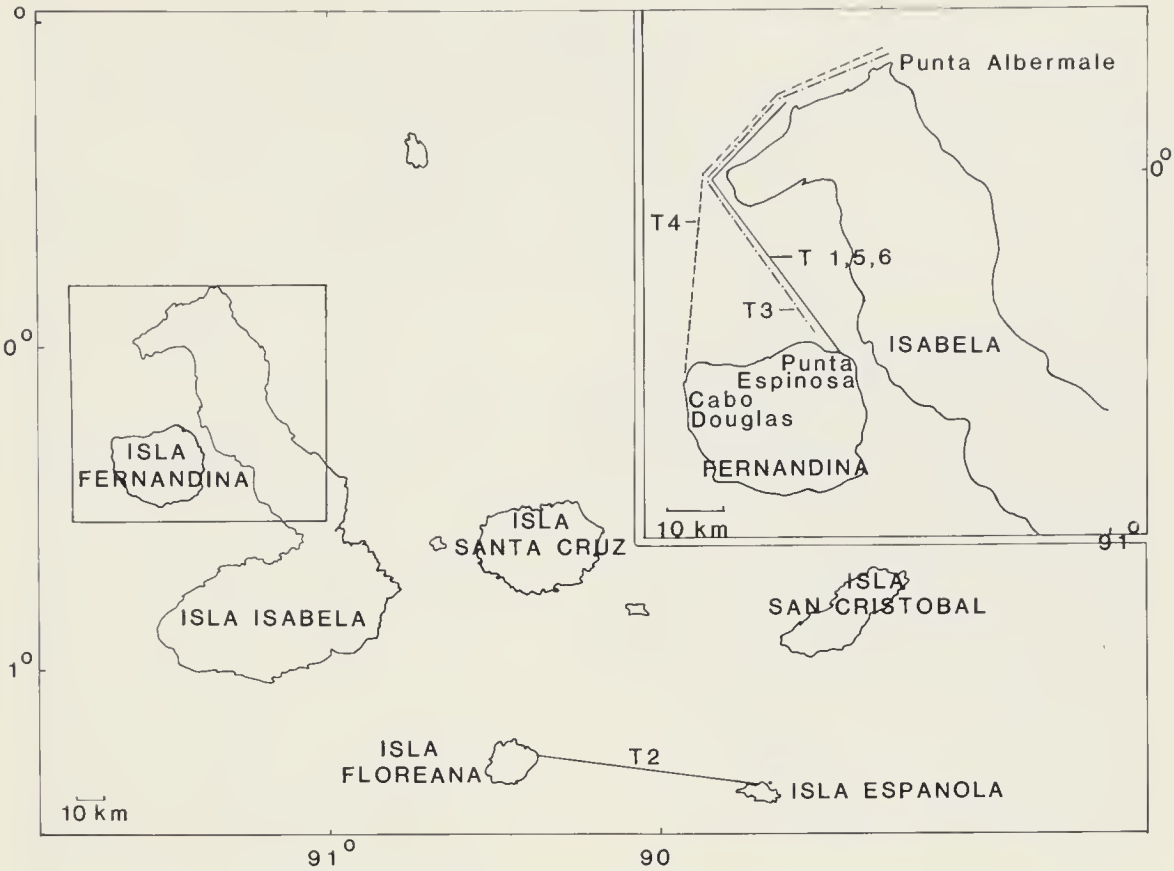


FIG. 1. Map of the Galapagos Islands showing locations of transects.

samples. An observer (GM) stood 4 m above the surface and counted all birds crossing a line perpendicular to the ship and extending out 300 m. All individuals and groups were recorded separately. We combined all records of frigatebirds because of the difficulties in distinguishing Magnificent and Great frigatebirds (cf. Harrison 1983).

Densities were calculated by dividing the total numbers of birds of each species seen by

TABLE 1

DURATIONS, DISTANCES, AREAS SURVEYED, AND SEA SURFACE TEMPERATURES FOR SIX TRANSECTS IN THE GALAPAGOS ISLANDS

| | Transect | | | | | |
|---|---|---|---|---|---|---|
| | El Niño | | | Post-Niño | | |
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Duration (min) | 171 | 182 | 68 | 133 | 93 | 29 |
| Distance (km) | 42.18 | 44.89 | 16.77 | 32.81 | 22.94 | 7.15 |
| Area ($km^2$) | 12.65 | 13.47 | 5.03 | 9.84 | 6.88 | 2.15 |
| Sea surface temperature (°C): | | | | | | |
| at start | 29.4 | 27.5 | 28.0 | 23.4 | 20.2 | 15.8 |
| midpoint | 29.4 | — | — | 24.0 | 20.3 | — |
| at end | 29.4 | — | 28.8 | 25.8 | 17.8 | — |

TABLE 2

DENSITIES OF BIRDS PER KM$^2$ DURING SIX TRANSECTS IN THE GALAPAGOS ISLANDS

| | Transect | | | | | |
|---|---|---|---|---|---|---|
| | El Niño | | | Post-Niño | | |
| | 1 | 2 | 3 | 4 | 5 | 6 |
| Species | | | | | | |
| Waved Albatross (*Diomedea irrorata*) | 0 | 0.5 | 0 | 0 | 0 | 0 |
| Galapagos Penguin (*Spheniscus mendiculus*) | 0 | 0 | 0 | 0 | 0.2 | 0 |
| Dark-rumped Petrel (*Pterodroma phaeopygia*) | 0.1 | 0.8 | 0.6 | 0 | 0 | 0 |
| Audubon's Shearwater (*Puffinus lherminieri*) | 1.3 | 0.2 | 5.0 | 15.8 | 0.3 | 37.2 |
| White-vented Storm-petrel (*Oceanites gracilis*) | 0.5 | 0.7 | 3.6 | 0.1 | 0 | 4.2 |
| Band-rumped Storm-petrel (*Oceanodroma castro*) | 0.1 | 0.2 | 0 | 0.1 | 0 | 0 |
| Wedge-rumped Storm-petrel (*O. tethys*) | 0.5 | 1.0 | 3.0 | 1.5 | 5.4 | 8.8 |
| Storm-petrel spp. (*Oceanites, Oceanodroma*) | 0.1 | 0.2 | 0.2 | 0.3 | 0 | 0 |
| Red-billed Tropicbird (*Phaethon aethereus*) | 0 | 0 | 0 | 0 | 0 | 0.5 |
| Brown Pelican (*Pelecanus occidentalis*) | 0.2 | 0 | 0.6 | 0 | 0.2 | 0.5 |
| Blue-footed Booby (*Sula nebouxii*) | 0.8 | 0.5 | 5.4 | 16.9 | 55.1 | 29.8 |
| Masked Booby (*S. dactylatra*) | 0.2 | 0 | 0.4 | 0.5 | 0.7 | 0.9 |
| Frigatebird spp. (*Fregata*) | 0.1 | 0.4 | 1.6 | 19.3 | 7.0 | 0 |
| Northern Phalarope (*Lobipes lobatus*) | 0 | 0 | 0 | 0 | 0 | 9.3 |
| Gull spp. (*Larus*) | 0.1 | 0 | 0 | 0 | 0.2 | 0 |
| Swallow-tailed Gull (*Creagrus furcatus*) | 0 | 0.1 | 0 | 0.1 | 0 | 3.3 |
| Brown Noddy (*Anous stolidus*) | 0.2 | 0 | 5.4 | 2.0 | 0 | 18.6 |

the area covered during a transect. Errors resulting from the small number of transects were minimized by using the entire transect length, rather than its subdivisions.

Transects (Fig. 1) were run on (1) 10 April 1983 (12:50–15:41 h) from Punta Espinoza, Isla Fernandina, to Punta "Atun," Isla Isabela; (2) 25 June 1983 (13:40–16:42 h) from Punta Suarez, Isla Española, to Punta Cormorant, Isla Floreana; (3) 1 July 1983 (12:15–13:23 h) from Punta Espinoza to Punta Albemarle, Isla Isabela; (4) 7 April 1984 (14:49–17:02 h) from Cabo Douglas, Isla Fernandina, to Punta Albemarle; (5) 4 January 1985 (12:23–13:56 h) from Punta Espinoza to Vincente Roca, Isla Isabela; and (6) 4 January 1985 (14:20–14:49 h) from Vincente Roca to Cabo Berkeley, Isla Isabela.

Transect 1 (Table 1) was run close to the time that El Niño was most severe (Feldman 1984); transects 2 and 3 were made later in the event. Subsequent transects were made approximately 10 and 18 months after the return of non-ENSO conditions to the area (Merlen 1985).

*Results and discussion.*—Audubon's Shearwaters (*Puffinus lherminieri*), Wedge-rumped Storm-petrels (*Oceanodroma tethys*), and Blue-footed and Masked boobies (*S. dactylatra*) were more abundant after, rather than during, El Niño; Brown Pelicans and White-vented Storm-petrels (*Oceanites gracilis*) appeared equally abundant in both periods; and Band-rumped Storm-petrels (*Oceanodroma castro*) and Dark-rumped Petrels (*Pterodroma phaeopygia*) were more abundant during El Niño than subsequently (Table 2). The higher numbers of the last 2 species during El Niño may reflect the fact that they fed closer to the islands

at that time, or that they experienced considerable mortality, depressing their numbers in later counts.

Group sizes of Audubon's Shearwaters (El Niño: $\bar{x} = 2.5 \pm 4.9$ [SD], N = 26; post-Niño: $\bar{x} = 19.75 \pm 44.4$, N = 12), and Blue-footed Boobies (El Niño: $\bar{x} = 2.9 \pm 2.1$, N = 18; post-Niño: $\bar{x} = 31.0 \pm 26.3$, N = 106) were consistently but not statistically larger after El Niaño (median and *t*-tests, corrected for unequal variances, $P > 0.10$). Patchiness or local abundance of prey resources must have been reduced greatly, because even such typical flock-feeders as Audubon's Shearwater and Brown Noddy (*Anous stolidus*) fed in smaller flocks or alone during El Niño.

Our results indicate that for some species such as Audubon's Shearwaters and Masked and Blue-footed boobies, adult emigration from Galapagos waters or mortality must have occurred during El Niño. If nesting failure alone had occurred, adults would have been present at sea. Although we do not have pre-Niño counts, the rapid increase in bird densities on transects since the end of El Niño suggests that most adult birds emigrated and returned, rather than died. Extensive adult mortality of seabirds during ENSO is known to occur in Peru, where thousands of birds wash onto beaches (Jordan and Fuentes 1966), but distinguishing between mortality and emigration may be more difficult in other systems. Regular transects and long-term studies of marked individuals are probably essential in such cases (e.g., Harris 1979). Additionally, we need more information on the diets and distributions of Galapagos seabirds under normal conditions so we can make inferences about changes in distribution caused by changes in resources during El Niño.

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David Cameron Duffy, *Percy FitzPatrick Institute of African Ornithology, Univ. Cape Town, Rondebosch 7700, South Africa;* and Godfrey Merlen, *P.O. Box 2542, Quito, Ecuador.* *Received 1 Nov. 1985, accepted 18 March 1986.*

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**Color variation in the Ruddy Duck (*Oxyura jamaicensis andina*).**—Males of the Ruddy Duck (*Oxyura jamaicensis andina*) of the Central and Eastern Andes of Colombia have been described and illustrated (e.g., Delacour 1959) as having mottled black-and-white cheeks that are intermediate between those of the large, black-headed *ferruginea* of the more southern Andes and the smaller, paler, and white-cheeked *jamaicensis* of the West Indies and North America. Adams and Slavid (1984) described a large amount of individual variation among *andina* drakes. Here, I present further details on this variation, obtained during field work in Colombia in 1981.

Detailed lateral view drawings were made of the heads of 20 drakes in nuptial plumage watched or photographed at close range in Laguna Pedropalo at 2000 m elev., Parque la Florida and Laguna San Ramon on the Bogotá savanna, 2600 m, and Lago Tota, 3020 m. This was supplemented by drawings of heads of 98 Ruddy drakes (including 41 *andina*) in nuptial plumage in the Museums of Natural History of Bogotá, Buenos Aires, Lima, and Santiago de Chile; the American Museum of Natural History; the Royal Ontario Museum

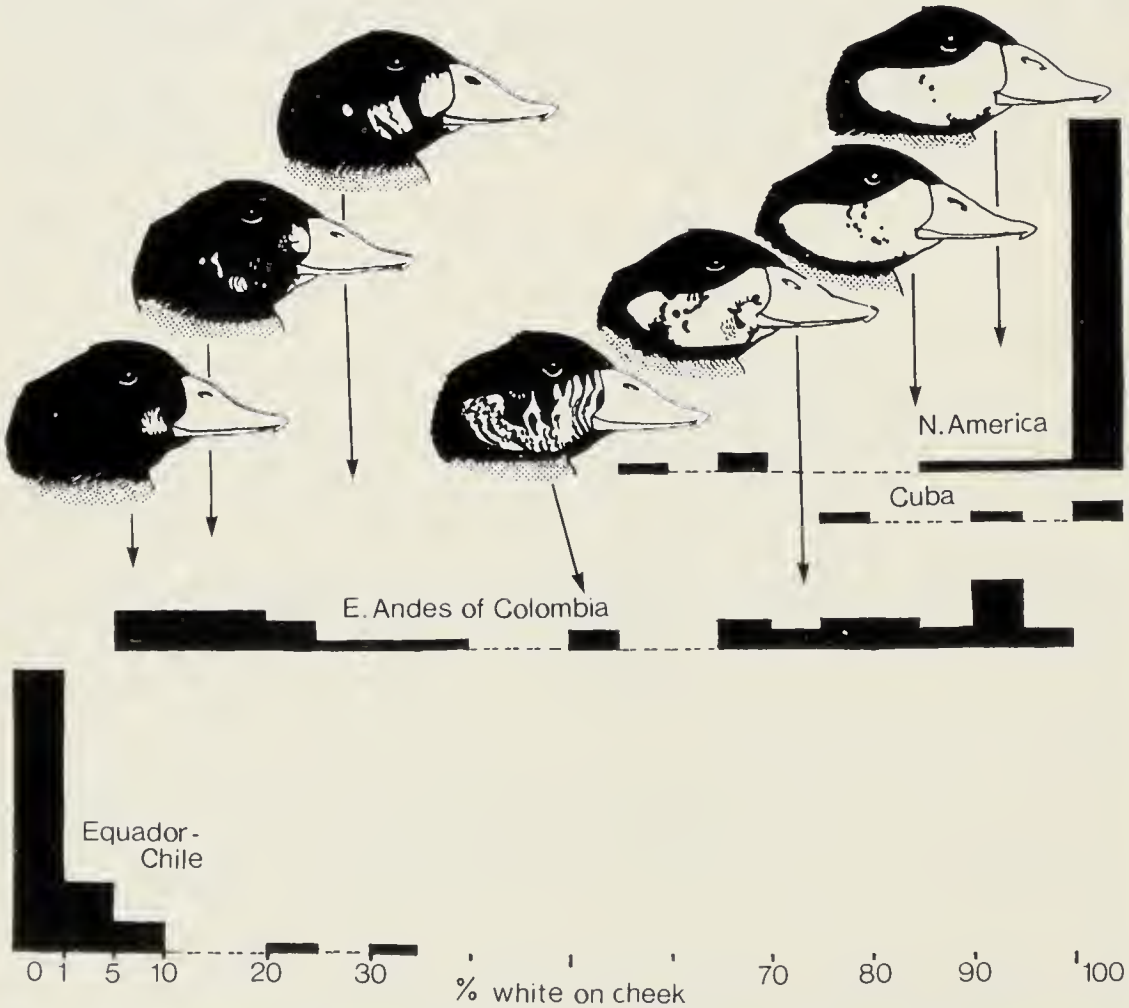


FIG. 1. Histograms showing percent white color on the cheeks of nuptial plumage drakes of Ruddy Ducks from North America, Cuba, the Eastern Andes of Colombia, and the Andes from southern Colombia to southern Chile.

(photos provided by J. C. Barlow); and the Zoological Museum of Copenhagen. This sample does not include birds with traces of basic plumage. The drawings were transferred to paper of homogeneous thickness, where the black and white segments were cut apart and weighed separately. This technique permits a fairly precise calculation of the relative amounts of white and black color. Little attention was paid to the colors of the body, as the variation is modest and is partly due to staining by iron oxides.

Figure 1 shows the patterns of oblique lines described by Adams and Slavid (1984). The lines are due to a rather homogeneous color along the individual follicle rows. Colombian drakes seem to be dimorphic, as the color patterns are normally polarized strongly towards either of the extremes. Some drakes are so dark-headed that white spots (on the lore and near the ear) are visible only on short range. Others are almost white-cheeked. Only two *andina* drakes are intermediate between *jamaicensis* and *ferruginea.*

Nearctic *jamaicensis* drakes are known to get some black cheek feathers during their prealternate molt, but these feathers soon fall out and the cheeks become white (Palmer 1976). This sequence is interesting considering the possible primitiveness of the black-cheeked condition suggested by Siegfried (1976). Individual variation in cheek color in *andina* may reflect individual variation in molt stage and hormonal balance. Dark and light *andina* drakes, however, courted females with apparently similar vigor and used similar postures. Also, the apparent bimodality of the variation, with both types represented in all nine months of the year from which data are available, contradicts this explanation. The presence of both types in all localities, as well as a similar frequency in 1981 data and in older museum specimens ($\chi^2 = 0.007$, df = 1, $P > 0.90$) suggest a rather stable situation.

The amount of individual variation suggests that *andina* is a hybrid population. Although the typical *jamaicensis* never visits South America today, it may well have reached Colombia in the Pleistocene and hybridized with *ferruginea,* perhaps in the wetlands that once covered the Bogotá plateau (van Geel and van der Hammen 1973).

The dimorphism could be due to a single allelic pair, or to assortative mating. Mate selection in waterbirds depends mainly on female choice, which may be under strong genetic influence (Walter 1973). As females were hard to tell apart individually, it was impossible to see whether they preferred particular drake types, and I have no direct evidence of assortative mating. In one locality, however, I recorded the color (five-category scale) of drakes that were within 1 m of each other and compared it with the combinations expected by random pairings. There was a tendency for dark drakes to be near each other ($\chi^2 = 10.55$, df = 1, $P < 0.001$) as well as for white-cheeked drakes to be near each other ($\chi^2 = 25.67$, df = 1, $P < 0.001$). The interpretation of this is unclear. Drakes may know their own appearance and prefer companions of similar type; they may prefer company of siblings; they may be influenced by early imprinting (cf. Bateson 1978); or they may be influenced by innate releasers (cf. Cinat-Tomsen 1926) coupled with their own morphotype.

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JON FJELDSÅ, *Zoological Museum, Univ. Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.* *Received 22 July 1983, accepted 24 June 1986.*

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**Systematic interpretations of foot-scute patterns in Neotropical finches.**—Past investigations of foot-scutes emphasizing North American taxa have documented taxonomic differences (Clark 1972, 1974, 1977). My more recent studies have emphasized several cases of taxonomic differences among those Neotropical finches traditionally placed in the Emberizinae. Here I summarize those differences and discuss their systematic interpretations, including consideration of the question of the affinities of the Galapagos finches with those of the mainland.

*Materials and methods.*—I examined more than 15,000 study skins of oscines, including representatives of more than 2400 species worldwide and samples of all genera of the Emberizinae, Cardinalinae, and Thraupinae. I also inspected 64 species representing all suboscine families except Oxyruncidae. All specimens were viewed either with a binocular dissecting microscope or a hand lens. The collections used are in the National Museum of Natural History (Washington, D.C.), the American Museum of Natural History (New York), the British Museum (Natural History) at Tring, the Yale University Peabody Museum of Natural History (New Haven), and the Museum of Natural History at the University of Connecticut (Storrs). My classification follows that of Morony et al. (1975).

*Sporophilines.*—Many Neotropical finches such as *Tiaris, Melanospiza, Lophospingus,* all the species of Galapagos and Cocos Island finches (geospizines), and all mainland genera of tanagers (Thraupinae) have a divided scute at the base of the two outer toes (scute E of Clark 1977) (Fig. 1A). Only in 5 genera, *Volatinia, Sporophila* (except *S. obscura,* discussed below), *Oryzoborus, Dolospingus,* and *Charitospiza,* is the lateral part of scute E most commonly fused with the most proximal scute on the outer toe (Fig. 1B). Such a fusion is not known to characterize any other passerine taxon. Morony et al. (1975) list 36 species in the 5 genera; I have examined representatives for all these except *Sporophila frontalis, S. ardesiaca, S. melanops, S. nigrorufa, S. insulata, S. palustris,* and *S. cinnamomea.* Some variant individuals within at least *Volatinia* and *Sporophila* show a *Tiaris*-like condition (Fig. 1A). For example, in a series of 58 specimens of *Volatinia,* 5 showed this *Tiaris*-like condition. In contrast, a *Sporophila*-like condition is apparently very rare as an individual variant in passerine species that typically have a *Tiaris*-like condition; I have seen one exceptional specimen of the tanager *Cnemoscopus rubrirostris* showing a *Sporophila*-like condition. The occurrence of such individual variations does not negate the potential taxonomic usefulness of species differences (Clark 1972).

The unique pattern of foot-scutes in the 5 genera might indicate their monophyletic origin. Olson (1981) summarized other evidence, including intergeneric hybridization (Sick 1963),

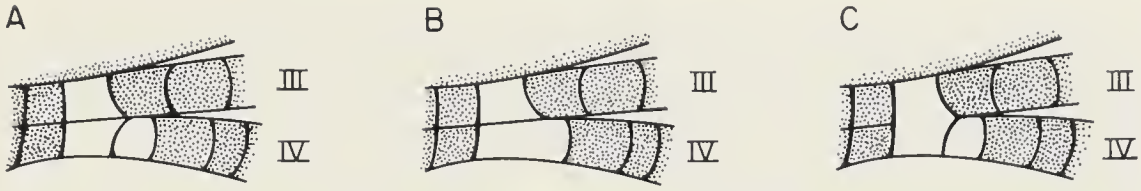


FIG. 1. Schematic dorsal view of the scutes at the base of the two outer toes in (A) *Tiaris*, (B) *Volatinia*, and (C) *Zonotrichia*. The region of differences is unshaded; see text for discussion.

indicating the close affinity of 2 of the 5 genera, *Sporophila* and *Oryzoborus*. Paynter and Storer (1970) placed the genera *Volatinia, Sporophila, Oryzoborus, Dolospingus,* and *Tiaris* within a group of 11 genera of thick-billed ground finches, but they considered this assemblage to be probably polyphyletic in origin. *Dolospingus* is a rare and little known monotypic genus from Venezuela and Brazil. Tordoff (1954) considered *Dolospingus* to be emberizine rather than cardueline on the basis of skull structure. *Charitospiza* is a poorly known monotypic genus from Brazil and northeastern Argentina. Miller (1928) believed that *Charitospiza* and *Lophospingus* were relatively closely related, but he noted a number of differences between them, to which may now be added the difference in foot-scutes. Paynter and Storer (1970) placed *Charitospiza* among their group of emberizines of uncertain affinities.

Historically, no structural characters have been found that would separate all emberizines from all tanagers (Thraupinae), but studies of DNA hybridization by Bledsoe (1985) indicate that 5 genera of finches traditionally considered to be emberizines, *Haplospiza, Diuca, Sicalis, Volatinia,* and *Oryzoborus,* are closer to traditional tanagers than they are to emberizines. Numerous Neotropical taxa including the geospizines have not been studied with respect to their DNA, but the DNA evidence does suggest that *Volatinia, Sporophila,* and *Oryzoborus* are evolutionarily well separated from many other traditional emberizines. The possibility that the similarity of foot-scutes in *Volatinia, Sporophila, Oryzoborus, Dolospingus,* and *Charitospiza* results from some convergence cannot be ruled out, but an hypothesis of homology is more parsimonious in the absence of contrary evidence.

*Sporophila obscura.*—This species differs from the other 23 examined species of *Sporophila* in having a *Tiaris*-like condition (Fig. 1A) at the base of the two outer toes.

The difference in scutellation between *S. obscura* and the other species of *Sporophila* matches their difference in nest structure and natal pterylosis. *S. obscura* builds a domed nest, unlike other *Sporophila* but like *Tiaris,* and hence Schwartz (in Paynter and Storer 1970) suggested that *S. obscura* should be placed in *Tiaris.* Collins and Kemp (1976) found that the young of *S. obscura* lack natal downs, like *Tiaris* but unlike other *Sporophila.* Nest structure and natal pterylosis might not be independent taxonomic characters in view of the tendency among avian taxa in general for sparse natal feathering to accompany enclosed nest sites. Foot-scutellation, however, also supports the hypothesis that *S. obscura* is misplaced in *Sporophila* and is better assigned to *Tiaris.*

*Affinity of geospizines with mainland finches.*—Steadman (1982) has summarized the comments of a number of earlier investigators who suggested, without citing many specific details, that the Galapagos finches arose from emberizines of the same stock that produced *Tiaris,* a widespread genus on the mainland, and the West Indian *Melanospiza.* One character shared by *Tiaris, Melanospiza,* and the geospizines is the building of a domed nest placed off the ground; *Tiaris* is the sole mainland genus of the traditional emberizines showing this behavior. The similarity, however, is rather simple and might be convergent (Steadman 1982).

In an extensive comparison, Steadman (1982) found that certain of the geospizines are more similar in osteology and plumage to *Volatinia* than to other traditional emberizines of the mainland. Steadman (1982) therefore reasonably proposed that the geospizines have evolved from *Volatinia*-like ancestors. Bledsoe's (1985) finding that *Volatinia* is a tanager raises the possibility that the geospizines are also tanagers. Barrowclough (1983), however, noted that the resemblances between *Volatinia* and the geospizines might be shared primitive features and hence perhaps misleading as to affinities. Thus there remains controversy concerning the relationships of the geospizines.

The difference in foot-scutes between *Volatinia* and the geospizines would not be expected under the hypothesis that *Volatinia* is the closest mainland relative of the geospizines. However, the difference in foot-scutes might have evolved after their divergence from a common ancestry. Further studies of DNA and other characters are needed to clarify the evolutionary radiation of these taxa.

*The* Myospiza *sparrows.*—As previously reported (Clark 1972), sparrows, juncos, towhees, and brush-finches placed in 23 New World emberizine genera (including *Zonotrichia, Ammodramus, Pipilo,* and *Atlapetes*) are characterized by an intact scute E at the base of the two outer toes (Fig. 1C). Species differences in presence or absence of an intact scute E in numerous other oscine families (Clark 1972, unpubl. data) indicate that this feature has been subject to considerable evolutionary convergence among oscines as a whole. Nevertheless, this feature in the emberizines is most parsimoniously interpreted as a shared, derived feature indicating a monophyletic origin of these 23 genera (Clark 1972). Further support for this interpretation is found in the close match between this group of genera characterized by an intact scute E and the group Ridgway (1901:27) characterized as having relatively small bills and plain coloration.

Among North American emberizine species with an intact scute E, only the Grasshopper Sparrow (*Ammodramus savannarum*) typically has 9 scutes on the middle toe (III), in contrast to the other species with 10 scutes (Clark 1974). In the present study I found this 9-scute condition in only 2 additional emberizines, the Grassland Sparrow (*A. humeralis*) and the Yellow-browed Sparrow (*A. aurifrons*), both Neotropical and together constituting a formerly recognized genus *Myospiza.*

Meyer de Schauensee (1966) considered the Grassland and Yellow-browed sparrows to be closely related. Mayr and Short (1970) commented that further study was needed of the relationship between the *Myospiza* sparrows and the Grasshopper Sparrow, and, in a phenetic osteological study, Robins and Schnell (1971) concluded that both the Grassland and Yellow-browed sparrows were appropriately placed in the genus *Ammodramus.* The evidence of foot-scutellation leads to the hypothesis that Grasshopper, Grassland, and Yellow-browed sparrows constitute a monophyletic group within a broader genus *Ammodramus.*

*General conclusions.*—Like other taxonomic characters, features of scutellation can constitute a shared and evolutionarily derived (synapomorphic) attribute in one case and yet be uninformative in another. This study, as well as previous studies (Clark 1977), indicates that foot-scutes, where useful in oscine systematics, are more likely to aid in recognizing affinities of closely related species and genera rather than at interfamilial levels.

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GEORGE A. CLARK, JR., *Box U-43, Dept. Ecology and Evolutionary Biology, Univ. Connecticut, Storrs, Connecticut 06268.* *Received 26 Sept. 1985, accepted 31 Mar. 1986.*

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**Northern Harrier predation on Willow Ptarmigan.**—There are few reports of Northern Harriers (*Circus cyaneus*) killing ptarmigan, although Braun and Rogers (1971) observed a harrier stooping on 2 White-tailed Ptarmigan (*Lagopus leucurus*). In North America, small mammals and birds comprise most of the diet of harriers (Watson 1977). In Scotland, however, Jenkins et al. (1964) found that harriers killed a substantial number of Red Grouse.

Here we document Northern Harrier predation on Willow Ptarmigan (*L. l. albus*) and detail the responses of the prey to presence of harriers during the breeding season in northern Canada. We suggest that harriers may be more important predators on ptarmigan, especially hens with nests, than has been reported previously.

Interactions between Northern Harriers and Willow Ptarmigan were observed in 3 populations in northern Canada between 1978 and 1985. A population of Willow Ptarmigan was investigated at La Perouse Bay near Churchill, Manitoba (58°24′N, 94°24′W), from 1981 to 1985 (Martin 1985). SJH studied populations of *L. l. albus* during 1978 at the

Anderson River Delta, Northwest Territories (69°42′N, 129°00′W), and *L. l. alexandrae* at the Chilkat Pass, Northwestern British Columbia (59°50′N, 136°30′W) from 1979 to 1985 (Hannon 1983). These areas are in subarctic, arctic, and subalpine tundra, respectively. Vegetation is open with shrub heights of about 50 cm in Manitoba and Northwest Territories and about 1 m in British Columbia.

Direct evidence of harrier predation on ptarmigan was observed 3 times. At La Perouse Bay, on 21 June 1985 at 09:35, DSH saw a female Northern Harrier flying slowly 5 m above 2 small islands 400 m distant. The harrier dove to the ground and was lost from view momentarily behind a small willow (*Salix* spp.) shrub. The harrier began to tear at something with its bill and when DSH was within 50 m, it flew away. The freshly killed carcass of a hen Willow Ptarmigan was found at the site. The breast and entrails were partially consumed and the head was still attached. The carcass was 40 cm from a ptarmigan nest containing 11 warm eggs. During this episode no cock ptarmigan was seen or heard. The next morning, the rest of the carcass had been removed and only the intact clutch and a number of ptarmigan feathers, mainly contours and rectrices, remained. On 22 July 1980, at the Anderson River site, a female harrier was observed dropping repeatedly on a brood of 10 recently fledged chicks and, despite being attacked by both ptarmigan parents, killing 4 chicks (T. W. Barry, pers. comm.). On 4 May 1979, at Chilkat Pass, SJH flushed a harrier off an intact carcass of a freshly killed yearling female Willow Ptarmigan.

We have also found rectrices or primaries of Northern Harriers at 6 kill sites on 3 areas (Table 1). Five kills were of females during egg laying and incubation, and the sighting at La Perouse Bay was of a hen at her nest. No bias was observed in ages of ptarmigan at these kill sites (Table 1). These observations are circumstantial evidence, as harriers may have been scavenging the carcasses (Watson 1977).

We observed ptarmigan responding to harriers 7 times during the breeding season. On 21 April 1985, at the Chilkat Pass, SJH observed a male harrier stoop at a territorial male ptarmigan, which jumped aside and called. The harrier flew on. On 17 May 1985 a female harrier flew over a resident pair of ptarmigan. The pair flew downslope; the cock gave a territorial call while the hen crouched under a bush after landing. At Anderson River (28 June 1978) an adult male ptarmigan was observed calling and then flying towards a harrier that had landed near it. The harrier flew away. On 30 June 1980, SJH watched an incubating female ptarmigan become alert and then "freeze" seconds before a female harrier flew over very low about 30 m from the nest. On 2 other occasions (12 June, 5 July 1982), KM observed harriers flying over nest sites at La Perouse Bay. In the latter case, the hen had been calling to her newly hatched chicks just prior to the overflight. In each case, both parents remained motionless and silent. On 5 July 1982, KM observed an adult female harrier repeatedly swoop over a single parent male Willow Ptarmigan with 10 2-day-old chicks. The cock lowered his wings and ran back and forth in front of the harrier. When the harrier landed on a 50-cm high willow, the male flew at it, wings dragging, neck feathers ruffled, tail fanned, and vocalizing intensely with "hisses" and "growls." The harrier swooped towards the brood about 6 more times before leaving, without capturing any chicks.

Ptarmigan are a relatively large prey item for harriers. In part, adult ptarmigan appeared to evade predation by aggressive responses to harriers. Berger et al. (1963) reported that when Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) on leks held their ground and attacked harriers, the harriers invariably retreated. Of 886 encounters, only one prairie chicken was killed. The authors concluded that, although harassment was common, harriers were not normally a serious threat. Both male and female Ring-necked Pheasants (*Phasianus colchicus*) have been observed to deter attacks by harriers (Weigand 1967, Carroll 1985).

During nesting, hen ptarmigan may be more susceptible than males to predation by harriers. Hens weigh less than cocks, and during incubation hens are at their lowest annual

TABLE 1
CIRCUMSTANCES IN WHICH HARRIER RECTRICES OR PRIMARIES WERE FOUND AT PTARMIGAN KILL SITES

| Date | Site | Stage of ptarmigan breeding season | Sex and age of kill[a] | Observer |
|---|---|---|---|---|
| 28 June 1978 | Anderson River | Late incubation | AF | SJH |
| 26 June 1979 | Chilkat Pass | Late incubation or early brood season | YM | SJH |
| 23 June 1984 | La Perouse Bay | Early incubation | AF | KM |
| 3 June 1985 | Chilkat Pass | Egg laying | AF | SJH |
| 19 June 1985 | Chilkat Pass | Mid incubation | YF | SJH |
| 26 June 1985 | Chilkat Pass | Late incubation | YF | SJH |

[a] AF = Adult Female, YF = Yearling Female, YM = Yearling Male.

weight (e.g., Chilkat Pass: females = 400 g, males = 470 g [Hannon and Roland 1984]; Anderson River: females = 525 g, males = 600 g [SJH, unpubl. data]; La Perouse Bay: females = 507 g, males = 617 g [KM, unpubl. data]). Female harriers weigh between 480 and 550 g (Scharf and Hamerstrom 1975). In addition, incubating female ptarmigan may not be able to scan for predators as well as males, and although concealed by vegetation, may be more vulnerable to detection by searching harriers.

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DAVID S. HIK, *Dept. Biology, Queen's Univ., Kingston, Ontario K7L 3N6, Canada;* SUSAN J. HANNON, *Dept. Zoology, Univ. Alberta, Edmonton, Alberta T6G 2E9, Canada;* AND KATHY MARTIN, *Boreal Inst., Univ. Alberta, Edmonton, Alberta T6G 2E9, Canada.* *Received 7 Jan. 1986, accepted 14 Apr. 1986.*

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**Predation on Black and Turkey vultures.**—Reports of predation on communally roosting or perching Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) are rare. Reported predation of vulture adults, eggs, and nestlings by mongoose (Scott 1892), fox (Howes 1926, Grube 1953), opossum (*Didelphis marsupialis*), and domestic dogs (*Canis familiaris*; Jackson 1983) took place at nests. We have also found canid scat and tracks in a freshly predated Turkey Vulture nest in Pennsylvania. Bald Eagles (*Haliaeetus leucocephalus*) sometimes pursue vultures, compel them to disgorge, and then consume the regurgitated material (Oberholser 1906). There is also a report of a Bald Eagle killing a vulture (Bent 1937). Although these reports indicate that vultures are susceptible to predation, we have been unable to find documentation of predation on vultures roosting or gathered in communal groups. Their large size, habit of roosting in tall trees, and congregation in large numbers seem to make Black and Turkey vultures unlikely candidates for predation. Here we report predation and what appeared to be attempted predation of communally perched and roosting vultures.

On 20 November 1984, at Gettysburg National Military Park, Pennsylvania, we observed what may have been attempted predation on Black Vultures by a Golden Eagle (*Aquila chrysaetos*). At 08:58 h, approximately 200 Turkey Vultures suddenly took off from a mixed flock of 300 Black and Turkey vultures perched in trees, on a fence, and in a pasture within 300 m of a permanent roost. The Black Vultures, which remained perched on the fence and ground, began shifting positions and looking up toward the sky. At 09:01 h an immature Golden Eagle stooped on the Black Vultures and chased one a short distance into the forest. The eagle then wheeled around and grabbed the back of a vulture still perched on the fence. Both birds fell to the ground. The vulture struggled free and flew off. The eagle perched on the ground as the remaining vultures took off and soared. After perching in a nearby tree for several minutes, the eagle landed on the ground and fed. The eagle departed at 09:33 h.

Upon investigation, we found that the eagle had been eating animal tissue containing several deer (*Odocoileus virginianus*) hairs. The material had the appearance and smell of meat recently regurgitated by vultures. Presumably the eagle attack caused one of the vultures to regurgitate its crop contents. Black Vultures regurgitate crop contents when disturbed, possibly as a defense mechanism (Jackson 1983). Whether the eagle was intent on catching a vulture or was pursuing the vultures to obtain regurgitated material is unclear. Our ob-

servations and the one by Oberholser (1906) suggest that regurgitation does not prevent attack by either Bald or Golden eagles, although it may distract pursuers.

On 5 April 1984, at Hopewell Furnace National Historic Site, we found 2 decapitated, but otherwise intact, vultures underneath a small group of trees in which vultures roosted regularly. During the winter approximately 100 Black and Turkey vultures roosted in these trees. The week before, however, only 15 to 20 vultures had been using the roost, probably because of dispersal to nesting areas (Coleman 1985). Although the roost area was frequented by visitors and park personnel, the dead birds had not been seen the previous day. This and the lack of tissue decomposition suggested that at least one of the birds had died that night. A necropsy showed heavy musculature, numerous subcutaneous fat deposits, and no signs of disease. Because there were no talon marks on the bird we concluded that mammalian predation, possibly raccoon (*Procyon lotor*), was the most likely cause of death. Park personnel reported finding 4 other decapitated and partially eaten Black Vultures in the previous 2 months.

Our observations suggest that predation on communally perched and roosting vultures may be more common than previously thought.

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John S. Coleman and James D. Fraser, *Dept. Fisheries and Wildlife Sciences, School of Forest and Wildlife Resources, Virginia Polytechnic Institute and State Univ., Blacksburg, Virginia 24061.* (Present address of JSC: *Florida Game and Fresh Water Fish Commission, 3991 SE 27th Court, Okeechobee, Florida, 33474.*) *Received 20 Feb. 1986, accepted 5 May 1986.*

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**Eastern Bluebird responses to nocturnal black rat snake nest predation.**—Rat snakes are well-known predators of cavity-nesting birds, and are known to kill incubating females and eat bird eggs and nestlings (e.g., Nolan 1959; Jackson 1970, 1977; Fendley 1980; Haggerty 1981). Rat snakes are reported to be major predators at Eastern Bluebird (*Sialia sialis*) nests (Fitch 1963, White and Woolfenden 1973). Studies of black rat snakes (e.g., Weatherhead and Charland 1985) have focused on diurnal activity patterns, and it is believed that diurnal observations alone accurately reflect rat snake densities (see Stickel et al. 1980). All accounts of nest predation by rat snakes concern diurnal or crepuscular observations. Here we document that black rat snakes (*Elaphe o. obsoleta*) are active after dark in the Ozarks and that they prey upon bluebird nests then.

We placed super 8-mm movie cameras with flash attachments on the backs of 6 Eastern Bluebird nest boxes during spring and summer 1985. Boxes were mounted at 1.5 m on fence posts along hayfields adjacent to a forested hillside near Durham, Washington County, Arkansas. A single frame picture of the inside of the entrance hole was taken when an infrared light beam was interrupted. Date and time of feedings were recorded for each visit by positioning a digital watch inside the box. Although designed to monitor parental feeding of nestlings, this technique also monitored predation events, and we filmed nocturnal predation by black rat snakes at 2 nest boxes.

On 26 May, a male bluebird made the last visit at 20:12 to a nest box that contained 1 11-day-old and 3 10-day-old nestlings. This was a west-facing box, and a faint trace of light could be seen behind the male in the picture. At 20:49, in complete darkness, a black rat snake was photographed entering the box. No additional information concerning this event was recorded; the snake must have remained in the infrared beam (i.e., in the entrance hole). The nest contained no nestlings the next morning at 06:47. The male bluebird continued to visit the empty nest box periodically until 15:28 on 27 May. The female was not recorded at the nest box after the nestlings disappeared.

On 9 August, a male bluebird made the last visit at 20:00 to a second nest box. We had removed the female from this box at noon that day to examine feeding rates of the male in the absence of the female. This nest contained 1 14-day-old and 3 15-day-old nestlings. A black rat snake was photographed entering the nest box at 01:44 on 10 August. At least one nestling greeted the snake at the entrance, in the manner that nestlings typically greet a parent bird (e.g., Thomas 1946). A series of pictures was taken. The snake, having consumed the nestlings, left the box 56 min after entering. At 06:36, the male bluebird returned to the empty nest box with a lepidopteran larva. He returned again at 07:49, 08:25, and 08:50, each time with a different grasshopper, after which he did not visit the box again.

When birds are breeding, rat snakes concentrate their foraging activity along habitat edges, such as fence lines (Weatherhead and Charland 1985). Of the 20 bluebird nests we studied in 1985 along fence lines, 12 nests, 11 of which contained nestlings, were preyed upon. At least 2 sets of nestlings were killed by House Sparrows (*Passer domesticus*) and at least 3 sets were eaten by black rat snakes. Due to the lack of disturbance at the other 7 nests, we suspect the eggs or nestlings were eaten by snakes. Six additional bluebird nests in boxes placed in fields away from fence lines suffered no nest predation.

Our results demonstrate that rat snake predation is possible at any time during day or night. The report of a radio-equipped fledgling Mourning Dove (*Zenaida macroura*) in a rat snake early in the morning (Mirarchi and Hitchcock 1982) also suggests nocturnal snake predation. Bluebirds may succeed at deterring rat snakes from preying upon nests during the day (Thomas 1946, Fitch 1963). Nocturnal attacks apparently go unchallenged by adults,

which do not spend the night in the nest cavity. The report by Fendley (1980) of dead ducks with broken necks in nest boxes associated with rat snake nest predation would suggest that it might be advantageous for adults to be absent during nocturnal snake visits.

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R. CRAIG HENSLEY AND KIMBERLY G. SMITH, *Dept. Zoology, Univ. Arkansas, Fayetteville, Arkansas 72701.* *Received 14 Jan. 1986, accepted 7 Apr. 1986.*

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**Destruction of heterospecific eggs by the Gray Catbird.**—Destruction of eggs by passerines is a relatively rare phenomenon that has been observed mainly in members of 2 closely related families: Troglodytidae (Belles-Isles and Picman 1986) and Mimidae (Bowman and Carter 1971, Temple 1978). Among North American mimids, 4 cases of egg destruction by the Gray Catbird (*Dumetella carolinensis*) have been reported (Pearson 1936, Bent 1948). Because egg destruction by this species was rarely observed, Bent (1948) concluded that such behavior was aberrant. Here we provide evidence showing that the behavior is more common than previously suggested.

The study was conducted in the summers of 1984 and 1985 at 2 sites in southern Ontario:

Presqu'ile Provincial Park (44°N, 78°W) and Mer Bleue Bog near Ottawa (46°N, 76°W). Catbirds from 10 territories (7 at the Presqu'ile Park, 3 at the Mer Bleue Bog) were involved in our experiments. From mid-June to mid-July we offered birds that were feeding nestlings eggs of Domestic Hens (*Gallus domesticus*), Common Quail (*Coturnix coturnix*), Blue-breasted Quail (*Coturnix chinensis*), Budgerigars (*Melopsittacus undulatus*), American Robins (*Turdus migratorius*), Yellow Warblers (*Dendroica petechia*), House Sparrows (*Passer domesticus*), and Common Grackles (*Quiscalus quiscula*) in American Robin, Yellow Warbler, Swamp Sparrow (*Melospiza georgiana*), Red-winged Blackbird (*Agelaius phoeniceus*), and Common Grackle nests. The choice of nests and eggs used during experiments was determined by their availability.

When adult catbirds were away from their nests, experimental nests with eggs were placed within 5 m (0.5–1.5 m above ground) of the catbird nests. During each experiment, one nest containing a single egg was offered to breeding catbirds (no more than one experiment per day per pair). A maximum of one trial per egg type was conducted on each breeding pair. We considered egg-pecking to be a positive response to the egg. We observed birds from at least 40 m from the experimental nests. Individual trials were continued for 2 h or until a catbird responded positively. All experiments were conducted between 14:00 and 19:00.

We observed egg destruction by catbirds in all 10 territories. In 6 territories, only one adult visited the nest. Because catbirds are sexually monomorphic we could not determine which adult pecked the experimental eggs. In the remaining 4 territories, however, we observed both adults pecking eggs. Catbirds responded positively in all 25 trials we performed. In all cases, catbirds responded almost immediately following their return to their nest by vigorously pecking the eggs. After pecking, catbirds usually removed a broken egg by picking it up and dropping it from the nest edge or carrying it several meters away. None of the birds were seen eating eggs they broke.

Results of a predation study conducted at Mer Bleue in July and August 1985 also suggest that egg-pecking by catbirds is relatively common, at least at unguarded nests. During the predation study, 18 automatic cameras were set near experimental nests with Blue-breasted Quail eggs. Movement of the eggs triggered a photograph of the manipulator. Experimental nests were randomly placed along 3 transects separated by at least 800 m. Birds destroyed 33 (31.1%) of the eggs. Catbirds and House Wrens destroyed 16 (15.1%) and 13 (12.3%) nests, respectively. Brown-headed Cowbirds (*Molothrus ater*) destroyed 3 eggs, and a Black-capped Chickadee (*Parus atricapillus*) destroyed one egg. Red squirrels (*Tamiasciurus hudsonicus*), short-tailed weasels (*Mustela erminea*), and raccoons (*Procyon lotor*) accounted for the remaining 73 (68.8%) depredated nests.

Gray Catbirds resemble Marsh Wrens (*Cistothorus palustris*), Sedge Wrens (*C. platensis*), and House Wrens (*Troglodytes aedon*) in their egg-destroying behavior (Picman 1977, Picman and Picman 1980, Belles-Isles and Picman 1986). Both males and females of these species peck and remove broken eggs from attacked nests and, in general, do not seem to consume their contents. Furthermore, all 4 species tend to destroy a variety of eggs in different nests. In contrast to the 3 species of wrens, catbirds did not remove any nest material during our trials.

Egg destruction by catbirds does not appear to be a form of food provisioning; however, by destroying the eggs of other birds Gray Catbirds might reduce competition for resources (cf. Verner 1975, Picman and Picman 1980, Belles-Isles and Picman 1986). The test of this hypothesis will require data on behavioral interactions between catbirds and other passerines, the degree of niche overlap among them, and the availability of resources important for their reproduction.

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Jean-Claude Belles-Isles and Jaroslav Picman. *Dept. Biology, Univ. Ottawa, Ottawa, Ontario K1N 6N5, Canada.* *Received 20 Nov. 1985, accepted 19 Mar. 1986.*

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**Fatal antipredator behavior of a Killdeer.**—Adult birds often defend their young against predators (Gottfried 1979, Gochfeld 1984). Distraction displays are one form of defense employed by parents, presumably at some risk to the performing bird (Barash 1975, Andersson et al. 1980, Greig-Smith 1980, Walters 1982). Increased intensity of distraction displays, and decreased distance from the potential predator, probably increase the risk to the performing bird (Barash 1975, Andersson et al. 1980). Despite the problem of habituation to intruders after repeated encounters, several studies show a correlation between the intensity of a distraction display and the vulnerability of offspring as indicated by nesting stage (Andersson et al. 1980, Lemmetyinen 1971).

Killdeer (*Charadrius vociferus*) are ground nesting birds that suffer heavy nest and hatching mortality (Nol and Lambert 1984). Killdeer antipredation strategies include cryptically colored eggs and chicks and the use of distraction behavior. Distraction behavior ranges from "false brooding" to "injury-feigning" (Gochfeld 1984). Direct, aggressive antipredator behavior by Killdeer is less common (cf. Deane 1944). Gochfeld (1984) named this type of aggressive behavior the "ungulate display." Birds performing this display move off the nest towards the intruder with their wings held slightly away from the body, and the contour

feathers fluffed. This posture becomes more exaggerated until the wings are held out at a considerable distance from the body, exaggerating the size of the bird. The tail is fanned and the cinnamon rump is exposed. The head is held in a lowered position. While in this crouched posture, the bird lunges towards the intruder in an apparent effort to halt its approach. In this paper I report on the use of a "threat display," which is directed towards predators of both adult Killdeer and their offspring. I also detail the fatality of a threat-displaying bird.

On 3 occasions I observed Killdeer respond to potential predators with a threat display. One case involved a red fox (*Vulpes vulpes*), and the other 2 instances involved humans. Each observation occurred during incubation and when the predator was within 5 m of the incubating bird. In 2 cases the Killdeer was a male and the clutch was within 2 days of hatching. The threat displays observed differed slightly from the ungulate display. The tail was held erect and not fanned. In 2 cases the threat displays were accompanied by a low pitched "growl" call, a call not described by Deane (1944). I was too far away from the bird during the encounter with the red fox to hear whether or not a call was given then.

In the case involving the red fox, the displaying bird was captured and killed by the fox. On 19 May 1985 at 06:30 h, I began observations of an incubating Killdeer from a car parked on a rise approximately 20 m from the nest. Neither adult of the pair had been banded, so I did not know the sex of the incubating bird. At 06:48 h the mate of the incubating bird flew to a feeding area approximately 1 km away. At 07:10 h a red fox approached the area of the nest from behind the incubating bird. When the fox was 2 m from the nest, the incubating bird showed signs of detecting the fox. The initial response of the bird was to run 0.25 m towards the fox in a threat posture. The Killdeer then quickly turned away and began injury-feigning, at which time it was pounced on and killed by the fox. The entire sequence of events lasted <30 sec.

I continued watching the nest for several hours after the attack, but, although there were Killdeer in the area, no bird returned to the nest. On returning later in the afternoon, I found that the clutch had been destroyed (shell fragments were found nearby).

To my knowledge this is the first documented case of a bird attempting to distract a predator and being captured and killed by that predator. Gochfeld (1984) suggests that individuals may minimize the risk involved in distracting a potential predator by keeping a safe distance from the predator. In order to remain at a safe distance an individual must be aware of the predator. When a predator is able to get very close to the nest without detection it seems likely that the nest will be discovered and predated. Therefore the "cost" to the surprised bird is high. In my observation the incubating bird was surprised by the predator. The initial response of the bird was to threaten the predator. My observation supports the assumption in the literature that distraction behaviors are performed at some risk of injury or death to the performer.

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DIANNE H. BRUNTON, *School of Natural Resources, Univ. Michigan, Ann Arbor, Michigan 48109.* *Received 12 Nov. 1985, accepted 3 May 1986.*

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**Plunge-diving by Olivaceous Cormorants in Chile.**—Seabirds employ a variety of foraging methods, but only surface-diving has been reported for cormorants (Phalacrocoracidae) (Ashmole 1971). We report here on plunge-diving by Olivaceous Cormorants (*Phalacrocorax olivaceus*) at Chiloé, Chile.

During 12–13 November 1985, in a sheltered, sand-pebble bay at Punta Puñihuil, at the south end of Mar Brava beach, on the west coast of Chiloé Island (41°55′30″S, 74°02′W), we observed 1–5 Olivaceous Cormorants foraging in water less than 2 m in depth. Three of the birds foraged by surface-diving, but 2 flew at maximum heights of 0.5 m above the water for 5–50 m before making low, oblique plunges into or in front of breaking waves of approximately 0.25–0.5 m high or into calm water 0.5–1.0 m depth. Birds plunged head first with their wings folded against their bodies, rather than folded behind the body as in gannets *Morus* spp. (Nelson 1978). Oblique plunges had a mean duration of 1.7 ± 0.6 sec [SD] (N = 20). Fish were caught during at least 2 plunges; additional fish may have been swallowed while the birds were underwater.

At the same time, Olivaceous Cormorants foraging by surface-diving in the same area remained underwater for 15.2 ± 4.4 sec, N = 12, similar to dive-durations in water <2 m deep in Peru (12.3 ± 4.5 sec, N = 36) (Duffy 1983), and in Texas, (16.0 sec) (Morrison et al. 1978). We saw 2 cormorants switch from surface-diving to plunge-diving and one switch back again.

Plunge- and surface-diving were used almost interchangeably, suggesting that both were effective methods of prey capture. The Olivaceous Cormorant is one of the most wide-ranging cormorant species (Blake 1977). The very unusual use of plunge-diving by a cormorant, in addition to normal pursuit-diving, may enable the bird to exploit food not normally available to cormorants.

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David Cameron Duffy, Rory P. Wilson, and Marie-Pierre Wilson, *Percy FitzPatrick Institute of African Ornithology, Univ. Cape Town, Rondebosch 7700, South Africa;* and Claudio Velasquez R., *Instituto de Zoologia, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.* *Received 7 Jan 1986, accepted 18 Mar. 1986.*

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**Which sex leads in paired Mallards?**—Among ducks the female is thought to determine the movements of the male during spring migration (Lincoln 1939). During courtship, drakes follow females in apparent attempts to establish and maintain pairbonds (Bellrose and Dzubin 1976), and hens lead when searching for a nest site or laying eggs (Sowls 1955). In Wilson's Phalaropes (*Phalaropus tricolor*) females commonly initiate "Paired Flights" (Howe 1975). Beecher and Beecher (1979) presented evidence that male Bank Swallows (*Riparia riparia*) follow their mates on flights from the burrow for a 7–8-day period following pair formation. They interpret these "chases" as a form of mate-guarding. I studied the relative positions of male and female Mallards (*Anas platyrhynchos*) moving between ponds by observing which sex led during takeoffs, flights, and landings.

Unmarked Mallards near Madison, Wisconsin, were studied from 12 March through 20 May 1977. Until 19 April, observations were restricted to a spring-fed pond at Nakoma Road Arboretum, which commonly held more than 40 Mallards. During mid-April, as the number of pairs decreased from at least 12 to about 7, I started to observe pairs at 4 other locations around Madison including lakes Monona, Wingra, and Mendota. Observations were made with 7 × 50 binoculars from a site 10–30 m from the shoreline. To exclude any possible influence of flights brought on by disturbance, no recordings were made during the first 5 min of each observation period. I used Lebret's (1961) characteristics for a pair on the water, as well as mutual head pumping, copulation with a male not associating with a courting party, and preening, feeding, and loafing in close proximity to distinguish paired birds. In flights, a drake and hen were considered paired when they alone approached the pond or lakeshore from a given compass direction. Thus, trios and larger groups were not included in my analysis.

Leading during takeoffs and landings was determined, respectively, by which individual's body was first to be completely out of or touching the water. In flight, the bird that was leading when a pair was first detected was deemed to be the leader. Subsequent changes in leadership were not recorded.

Females led pairs in 85% of the takeoffs (35 of 41 observations), 83% of in-flight obser-

vations (104 of 125), and 62% of the landings (60 of 97). For all 3 situations females led significantly ($P < 0.025$) more often than expected by chance. Takeoff and in-flight data are not statistically different from each other ($\chi^2 = 0.11$, df = 1, $P > 0.5$), but both differ significantly from landing (takeoff vs landing: $\chi^2 = 7.43$, $P = 0.006$; in-flight vs landing: $\chi^2 = 12.89$, $P < 0.001$). Percentages remained constant throughout the study period (8 periods tested against overall proportions: takeoff: $\chi^2 = 0.50$, df = 7, $P \geq 0.50$; in-flight: $\chi^2 = 0.62$, df = 7, $P > 0.50$; landing: $\chi^2 = 6.87$, df = 7, $P > 0.10$).

The male, if leading in flight, subsequently landed first 13 of 18 times (72%) in which both situations were observed. When females led in flight, males subsequently landed first 25 of 79 times (32%; $\chi^2 = 10.13$, df = 1, $P < 0.005$).

Females may lead in flight because of greater nutritional and energetic constraints on breeding female waterfowl (Krapu 1974, Titman 1981) or, if males are mate-guarding, females may lead by default, as the guarding sex must respond to the movements of the sex that is being guarded. At no time does there appear to be a consistent advantage for male leadership, except during landing, when male choice of a landing site may minimize attempts of forced copulation (Burns et al. 1980; Stewart and Titman 1980) by keeping his female away from other males. Some males appeared to lead females away from landing near other males on the water (pers. obs.; Dzubin, pers. comm.). Females may lead in landings less than in flights because males descend faster or because males pick the local landing spot and lead the female to it.

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Kim C. Derrickson, *Dept. Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.* *Received 12 Nov. 1985, accepted 18 Mar. 1986.*

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**Ages of mated pairs of California gulls.**—Several studies of long-lived seabirds have shown that mated pairs are usually the same or nearly the same age. For example, Coulson and Horobin (1976) report ages of 29 pairs of Arctic terns ranging in age from 3 to 18 years old. Eighty-three percent of mated pairs differed in age by no more than 2 years. Mating of similar-aged individuals has been reported for a number of other species (e.g., Yellow-eyed Penguin [*Megadyptes antipodes*], Richdale 1957; Kittiwake [*Rissa tridactyla*], Coulson 1966; Red-billed Gull [*Larus novaehollandiae scopulinus*], Mills 1973; Fulmar [*Fulmarus glacialis*], Ollason and Dunnet 1978; White-fronted Tern [*Sterna striata*], Mills and Shaw 1980; Common Tern [*Sterna hirundo*], Nisbet et al. 1984). Here we describe ages of mated pairs of California Gulls (*Larus californicus*) and discuss possible explanations that may account for high correlation in ages of mated pairs.

*Methods.*—Data were gathered in 1979 and 1980 on California gulls breeding on an island on Bamforth Lake, Wyoming. Detailed descriptions of the breeding colony and nesting habitat are in Pugesek and Diem (1983).

Gulls from the Bamforth colony have been banded and wing-marked as nearly fledged chicks almost every year since 1958. Gulls were watched on the breeding island in 1979 and 1980 as they defended nesting territories. Their leg band or wing marker numbers were

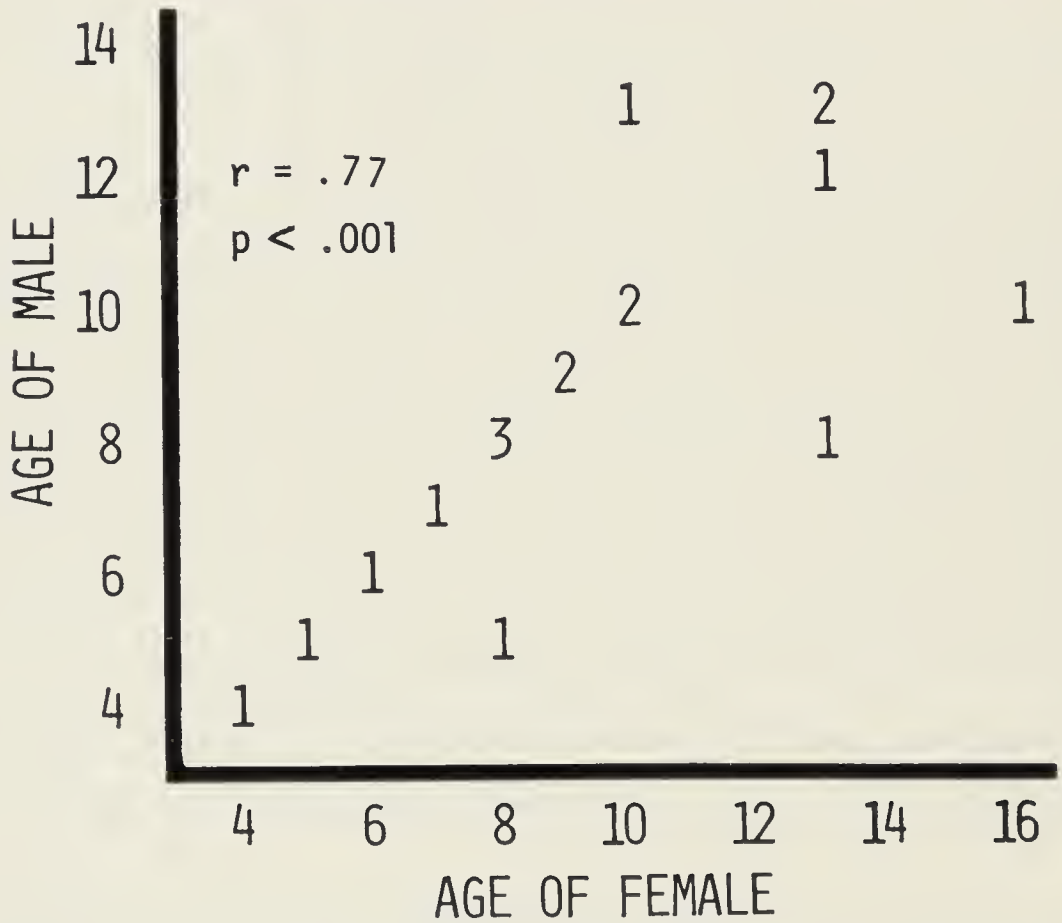


FIG. 1. Age of male and female mated California Gulls with Pearson's Correlation Coefficient and significance level. Numbers designate pairs found with a particular age combination (N = 18 pairs).

read with the aid of a spotting scope and the nesting territory marked with a coded stake (8 × 2 × 40 cm). We returned to staked nest sites at various intervals to determine whether mates were also banded. Gulls were aged by banding records. Sex was determined by bill characteristics (bill length, head-bill length, and bill depth) (Fox et al. 1981, Diem, unpubl. data) recorded at the time of banding. Gender was further verified by visual comparisons of mates at the nest site. Males are usually larger than females and can be distinguished from females in side-by-side comparison of bill characteristics. In all cases, gender, as determined by such comparisons, agreed with that determined by previous bill measurements.

*Results and Discussion.*—Breeding adults in the Bamforth colony range in age from 3 to 20 years old (Pugesek and Diem, unpubl. data). Despite the wide variation in ages of potential mates, gulls nearly always mated with individuals of the same age (Fig. 1). In 13 of 18 pairs (72%), mates were born in the same year. Mates were within 3 years of age in 16 of 18 pairs (89%). Results, therefore, are consistent with those reported for other seabird species.

The similarities in ages of mates could occur for a number of reasons. In gulls, timing of reproductive readiness varies with age. For example Mills (1973) found that older Red-billed Gulls come into reproductive condition before younger gulls. A similar condition is likely in the California Gulls at Bamforth Lake as oldest members of the population are first to arrive in the breeding area, and establish nesting territories (Pugesek 1983). Thus if variation in the date at which gulls are physiologically ready to accept mates differs between age-classes, gulls would only find mates of the same age. The process of pairing similar-aged individuals may be further augmented by retention of mates from year to year (Coulson 1966).

It is unlikely, however, that timing of reproduction and retention of mates are sufficient to explain the high degree of correlation in ages of mated pairs observed during our study. Considerable variation occurs within age classes in behavior and timing of reproductive events (Pugesek 1983). Many young gulls establish territories, incubate, and hatch eggs before older gulls. For example, mean hatching date of the youngest gulls (3–6 years old) was only 4 days later than that of gulls 11 years and older. Standard deviations in hatching dates were 5.0 and 5.5 days, respectively, indicating a high degree of overlap between age groups. Presumably, a similar amount of overlap occurs between age groups in the date of pair formation. Nisbet et al. (1984) came to a similar conclusion that timing of reproduction was not sufficient to explain high correlation in mate ages. In addition, frequency of mate retention is low on the Bamforth colony. For example, only one of 5 banded pairs observed in 1979 was with the same mate in the following year. Had individuals paired at sexual maturity and remained together for life, mate retention would result in high correlations in mate ages. However, as mate retention is not life-long, its tendency to produce correlation in mate ages is greatly reduced.

Considerable age-related variation occurs among California gulls in parental behavior. Reproductive effort and fledging success increase with age (Pugesek 1981, 1983; Pugesek and Diem 1983). Consequently, mate selection may also be based on age. Individuals may actively select mates (after Parker 1983) based on their age and potential for reproductive investment. Further investigation is required to determine the mechanism(s) which result in a high correlation in ages of mates.

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BRUCE H. PUGESEK, *Dept. Biological Sciences, Purdue Univ., West Lafayette, Indiana 47907;* AND KENNETH L. DIEM, *Dept. Zoology and Physiology, Univ. Wyoming, Laramie, Wyoming 82071.* *Received 1 Nov. 1985, accepted 20 May 1986.*

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**Aerial rain bathing by Common Nighthawks.**—Both Slessers (Auk 87:91–99, 1970) and Simmons (pp. 101–104 *in* A Dictionary of Birds, B. Campbell and E. Lack, eds., Buteo Books, Vermillion, South Dakota, 1985) classified methods of bathing in water by birds, but neither mentioned a method we observed in the Common Nighthawk (*Chordeiles minor*), and here named "aerial rain bathing."

At about 12:00 EDST on 10 August 1985 a thunderstorm with heavy rains passed over the Archbold Biological Station in Highlands County, Florida. During the next 45 minutes, 43 mm of rain fell locally and west winds gusted up to 37 km/h. From inside the laboratory building we watched a flock of about 15 nighthawks flying in the heaviest downpour. They flew about 10 to 35 m above oak scrub and among and above scattered slash pines (*Pinus elliottii*), where we think they had been roosting before taking flight.

The flight of the birds was different than usual: they often glided in place as they all faced into the wind, with their body plumage ruffled and tails slightly spread. They appeared to fly with slower wing beats than normal, but several times gave short series of quick beats.

No nighthawk dived or flew erratically as in normal foraging, although individuals did circle back to regain their previous positions. During the approximately 10 minutes of flying in the rain, the flock remained in the same area. When the rain slackened the birds all flew off to the west.

We interpret these observations as aerial rain bathing. The ruffled plumage and spread rectrices may have facilitated feather soaking. The quick wing beats may have functioned to shake water off the wings. Certainly, the birds were not foraging; we doubt that any insect could have remained aloft in the heavy rain. In addition, none of the aerial movements resembled any described display behavior. We heard no calling when we ventured outside the building.

Many birds bathe in rain or wet foliage. No doubt characteristics of birds and their habitats affect the distribution of this form of bathing. Birds that are poorly adapted for standing in water because of short tarsi or weak legs, or that are unable to swim, probably bathe in rain or wet foliage. Birds that live where standing water is inaccessible, or where rain or dew are frequent also probably bathe in rain or wet foliage. GEW once watched a captive frogmouth, *Podargus* sp., a rain-forest bird with short tarsi and weak legs, bathe in the falling spray of a garden hose. The posture of rain-bathing birds "with feathers ruffled, wings fully extended horizontally, and tail spread" (Simmons 1985) certainly characterized the nighthawks we watched, and supports our conclusion that they were bathing in the rain.

Strong flying land birds such as kingfishers and tyrant flycatchers bathe by plunging into the surface of standing water. Simmons (1985) described "flight bathing on the wing by a series of dips and rises," and gave as examples swifts and swallows. He further stated that "highly aerial seabirds, such as frigatebirds and certain terns, are solely flight-bathers." By the context we suspect Simmons is referring to dips *into water* when describing flight-bathers, but we are uncertain. Certainly the several taxa of land birds and seabirds he listed include likely candidates for aerial rain bathing. Among other likely candidates are hummingbirds. Stoner (Condor 49:36, 1947) reported an Anna's Hummingbird (*Calypte anna*) repeatedly flying through a stream of water from a garden hose, which may be interpreted as bathing while in flight.—KEVIN J. MCGOWAN AND GLEN E. WOOLFENDEN, *Dept. Biology, Univ. South Florida, Tampa, Florida 33620.* *Received 13 Dec. 1985, accepted 6 May 1986.*

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**Green-backed Heron baits fish with insects.**—On 22 August and 8 September, 1985, we observed at least one Green-backed Heron (*Butorides striatus*) apparently attempt to lure fish with live mayflies (Ephemeridae) at the Ouachita River in Montgomery County, Arkansas. On 3 separate occasions, in 3 locations, we watched a heron capture a live mayfly and place it in the water. After the heron watched the mayfly for several seconds from a crouched, standing posture (Hancock and Kushlan 1984), it retrieved the live insect and placed it in a new location in the water a few feet away. This pattern was repeated 10–20 times for up to 30 min before the heron abandoned the mayfly and flew out of sight. We did not witness a heron capture a fish while baiting.

Kushlan (1978) described baiting behavior as placing any material that attracts prey in the water. Lovell (1958), Sisson (1974), and Norris (1975) previously have documented Green-backed Herons baiting fish with bread and feathers. To our knowledge, this is the first report of this species using an insect as bait.

Insects are frequent prey of Green-backed Herons in late summer (Niethammer and Kaiser

1983). If mayflies are natural prey of Green-backed Herons, our observations carry intriguing implications regarding optimal foraging theory. Theorists predict that, when prey densities are high, a predator will usually select the more profitable of 2 prey when given a choice between them (see Krebs et al. 1983 for review). In the present case, the Green-backed Heron risked one potential prey item in an attempt to secure larger, presumably more profitable prey. Mayflies were widespread and abundant during our observation period, and baiting with mayflies was probably a "low-cost" behavior.

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CHARLES R. PRESTON, *Dept. Biology, Univ. Arkansas at Little Rock, Little Rock, Arkansas 72204;* HERSHEL MOSELEY AND CAROLYN MOSELEY, *11123 Shannon Hills Dr., Mabelvale, Arkansas 72103.* *Received 31 Jan. 1986, accepted 1 May 1986.*

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**Great-tailed Grackle kills Barn Swallow in flight.**—On the causeway from Port Isabel to South Padre Island, Cameron County, Texas, at dusk on 9 April 1985 I noticed a flock of 8–12 Barn Swallows (*Hirundo rustica*) flying 1–4 m above the mudflats near the end of the bridge and just south of it. As I watched, two female Great-tailed Grackles (*Quiscalus mexicanus*) flew up behind this flock. One of the grackles struck one of the swallows and drove it to the ground. The grackle then pecked the swallow and dragged it by one wing for ca 0.5 m as the other grackle watched. Both grackles then flew away.

After the grackles departed, 6 swallows remained flying over the mudflat at 18:00 h. I then retrieved the dead swallow (USNM 599917) which was autopsied and prepared by Joe T. Marshall. The bird was a male. A hemorrhage was present on the left frontal bone but the skull was unbroken in this area. There was a gaping hole behind the left ear. Although the grackle had pecked at the breast several times there was no obvious injury in this area.

Grackles (*Quiscalus*) are frequent predators of other bird's eggs and young (Bent 1958), but rarely have been reported killing adults. Great-tailed Grackles have killed adult House Sparrows (*Passer domesticus*) (Hansen 1976), and Common Grackles (*Q. quiscula*) have frequently been reported killing this species (Poor 1946, Mayfield 1954, Taylor 1958). Common Grackles have been reported killing a Dickcissel (*Spiza americana*) (Baird and

Smith 1965), an American Robin (*Turdus migratorius*), and a Gray-cheeked Thrush (*Catharus minimus*) (Townsend *in* Bent 1958).

Resting swallows have been killed by both Boat-tailed Grackles (*Q. major*) (McIlhenny 1937) and Common Grackles (LaPorte 1974), and a foraging Barn Swallow was taken in flight by a California Gull (*Larus californicus*) (Laymon 1983). At least 2 similar acts of predation have been reported for Common Grackles. One grackle was seen killing an immature Cedar Waxwing (*Bombycilla cedrorum*) as the latter fed in flight (Fisk 1970); another killed an immature Cedar Waxwing that had just been released by a bander (Ritchison 1982).

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Roger B. Clapp, *Biological Survey Section, U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.* *Received 8 Mar. 1986, accepted 6 May 1986.*

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# ORNITHOLOGICAL LITERATURE

NEOTROPICAL ORNITHOLOGY. By P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.). Ornithol. Monogr. 36, American Ornithologists' Union, Washington, D.C., 1985:xi + 1041 pp., 7 colored plates. $70.00 (Order from Frank R. Moore, Assistant to the Treasurer, A.O.U., Dept. Biology, Univ. Southern Mississippi, Southern Station Box 5018, Hattiesburg, Mississippi 39406.)—Dedicated to Eugene Eisenmann and offered as a permanent memorial to his broad and lasting influence on Neotropical avian biology, this heavy volume represents a landmark contribution. Assembled here are 63 papers by 79 authors representing scores of institutions in the United States, Middle America, the West Indies, South America, and Europe. In the introductory paper, Thomas R. Howell reviews Eisenmann's remarkable life and his multifaceted contributions to the study of Neotropical birds. The next 61 papers are organized under eight headings: "New Taxa" (5 papers), "Zoogeography and Distribution" (11), "Systematics" (9), "Evolution" (10), "Community and Population Ecology" (10), "Evolutionary and Behavioral Ecology" (8), "Breeding Biology" (3), and "Conservation" (5). Thus, the coverage heavily emphasizes Eisenmann's own interests. Each paper begins with an Abstract, in both English and Spanish, and ends with a list of Literature Cited. Kenneth C. Parkes analyzes the contents of the entire volume in the final paper, "Neotropical Ornithology—An Overview." An Index lists key words that reflect the subject matter covered, names of contributors and artists, and the scientific names of newly described taxa. The vivid colored plates (by J. W. Fitzpatrick, D. Gardner, R. M. Mengel, J. P. O'Neill [2], R. T. Peterson, A. Singer, and M. D. Williams) either depict previously undescribed taxa and their close relatives or illustrate other species under discussion. Tables, graphs, maps, and appendices abound. There are relatively few photos.

With a text composed of fine, dense print and narrow margins, the 1041 pages of "Neotropical Ornithology" contain an awesome amount of information. In terms of new data, novel interpretations, and general information conveyed per page, the present volume far surpasses "Biological Diversification in the Tropics" (G. T. Prance, ed., Columbia Univ. Press, New York, New York, 1982), an inflated although comparably expensive tome on a related but broader topic.

Although symposium volumes, Festschrifts, and the like typically suffer from unevenness in quality, the contributions in this book are consistently of high caliber, a tribute to the toil and dedication of the five editors and their 125 (!) reviewers. Indeed, the attention to detail that characterizes genuine scholarship is evident throughout. Appropriate statistical tests routinely are applied where necessary. I was especially pleased to note the abundance of hard data in tables and appendices. Previously unreported information (e.g., on nest characteristics, body weights, and colors of soft parts) is presented for many species. In a number of papers, detailed accounts describe new records and provide natural history notes on unusual species. Inevitably, more than a few of these accounts will become epitaphs over the next decade as the shadow of habitat destruction lengthens across the Neotropics.

Space allotted here precludes comment on most of the individual papers. Moreover, Parkes has already accomplished this in his comprehensive overview. However, of the many solid contributions, two impressed me as masterworks, deserving of special comment. The first, by John W. Fitzpatrick, concerns the radiation of the Tyrannidae. In an analysis of 94 living species (25% of the family), he examines possible relationships between site and style of prey capture and measurements of the bill, wing, tarsus, and tail. Generalized foragers have generalized morphologies; species with peculiar feeding modes are characterized by deviant

physical measurements. Members of these two extremes are joined by species at various intermediate stages of specialization in feeding and structure. Thus, from the close correspondence between behavior and morphology seen in living species, we can infer the nature of ancient phyletic avenues along which New World flycatchers radiated from generalists, through intermediates, to diverse kinds of specialists. The relatively competitor-free environment in which the suboscines may have radiated could have provided the setting that encouraged their impressive diversification. Fitzpatrick concludes that, ". . . today's family Tyrannidae may illustrate pathways of morphologic and behavioral specialization long since obliterated in most other modern bird families." Although this method of phylogenetic reconstruction is not new, I know of no other example in birds where it has been applied with such clarity and thoroughness.

A second notable paper, by Timothy C. Moermond and Julie Sloan Denslow, exhaustively reviews (173 references) Neotropical avian frugivory. The topic turns out to be far more complex than many previous workers have implied. From consideration of a wide array of taxa, the authors found no consistent morphological adaptations for the digestion of fruits; instead, specializations in digestive physiology seem likely. Small birds (e.g., tanagers and manakins) mainly eat fruits rich in carbohydrates. Large species (e.g., cotingas and toucans) consume a wider range of fruit sizes, from small, carbohydrate-rich kinds to large fruits rich in lipids. Modes of fruit-picking and processing are extremely diverse. A major finding is that very few species can both reach fruit easily while perched and pick fruits with facility while in flight. Morphologic and behavioral correlates of fruit foraging are carefully documented and discussed. Tables and figures provide data on wing loading, body weight, specific muscle weight, and other relevant variables. Finally, only a very few species (Oilbirds [*Steatornis caripensis*] and a few cotingids) appear to be totally frugivorous. Thus, the dogma that fruit-eating birds can be divided neatly into either generalists or specialists on the basis of diet, behavior, or morphology should perish as one more unsupported oversimplification. These points are merely the highlights of a very scholarly and insightful analysis that is bound to be widely cited.

In the Preface the editors state that, "Wherever we have been able to induce authors to do so, we have sought comparisons between tropical and temperate zones . . . , and between paleotropical and neotropical birds and ecosystems." Unfortunately, only a few papers satisfy these worthy objectives. For example, both Murray and Skutch discuss latitudinal variation in clutch size, Remsen compares the highland avifaunas of two sites in Bolivia with one in the White Mountains, New Hampshire, and Kushlan et al. contrast the wading bird community of the Venezuelan Llanos with that of the Florida Everglades. Only Houston's essay on the evolutionary ecology of Afrotropical and Neotropical forest vultures, and Short's contribution contrasting radiations of barbets and woodpeckers in the New World tropics versus the Old World tropics, offer intercontinental tropical comparisons. Thus, despite the publication of "Neotropical Ornithology," there remains the need for direct latitudinal and intertropical comparisons of a host of features for which avian data are amenable, including migration, pairbonding, territoriality, breeding cycles, molting, plumages, and subspeciation. The profound differences between Paleotropical and Neotropical environments described in Prance (1982) further underscore the need for additional comparative studies. Nonetheless, the shortage of geographic comparisons in "Neotropical Ornithology" is not a serious weakness; future workers will undoubtedly conduct such investigations as new information accumulates. In the meantime, Ricklefs and Bloom's analysis (Auk 94:86–96, 1977) of latitudinal trends in several life history parameters serves as a model for the kinds of comparisons that hopefully will become more commonplace.

In sum, the publication of this admirable and important book introduces a new era in

the study of Neotropical ornithology. Because it is certain to influence research on tropical birds far into the future, the volume belongs within easy reach of every ornithologist and tropical biologist regardless of their specific interests.—NED K. JOHNSON.

THE BEGINNINGS OF BIRDS. PROCEEDINGS OF THE INTERNATIONAL ARCHAEOPTERYX CONFERENCE EICHSTÄTT 1984. By M. K. Hecht, J. H. Ostrom, G. Viohl, anad P. Wellnhofer (eds.). Freunde des Jura-Museums Eichstätt, Willibaldsburg, D-8078 Eichstätt, Federal Republic of Germany, 1985:342 pp., numerous black-and-white illustrations. D.M. 90 (D.M. 93 outside of Germany).—Probably no fossil form has been written about as much as *Archaeopteryx,* the classic evolutionary intermediate. This book records the proceedings of a 1984 conference of workers from a variety of discipines, and was held, most appropriately, in the center of the quarry district from which all five specimens have come. Hopes for a general consensus on major questions generally were not realized. There is considerable variation in the quality of the contributions; although many are highly original, some are restatements of previous ideas. Many topics are addressed in the 38 papers, but space limits emphasis here to a few main questions and authors.

How did birds begin to fly? One popular idea is the cursorial or "upwards" theory that running (or hopping) prebirds began by jumping into the air to reach insect prey or to escape predators, using incipient wings to lengthen their time aloft. The main alternative is the arboreal or "downwards" theory that flight evolved in forms that leaped from trees, and passed through successive parachuting and gliding stages to powered flight. These theories are reviewed and tinkered with repeatedly in this volume, and plausible arguments for both are presented. Perhaps the most useful new anatomical analysis is Yalden's argument that the clawed fingers of *Archaeopteryx* were adapted to permit it to climb trees like a squirrel. One variation on familiar themes is the idea of Peters that avian ancestors glided down hilly slopes, thus reconciling the apparent open habitat with the advantage of using rather than fighting gravity. More unusual is the theory of Thulborn and Hamley that *Archaeopteryx* was a wader that used its wings as a canopy like herons do, and that flight originated in forms that fluttered from wave crest to wave crest. In addition to studies based mainly on *Archaeopteryx,* there are several more theoretical analyses of flight in general. Some of these are firmly grounded in anatomy and mathematics, others are merely armchair speculations. In general, it cannot be said that agreement was reached on the origin of flight, but the downwards theory appears more popular.

A second question deals with the origin of feathers. It is generally agreed that they evolved from reptilian epidermal scales, but there has been a dispute about their original function. One theory is that feathers originated for flight and subsequently were adapted for thermal insulation. In this volume Feduccia defends this theory partly on the grounds that the complexity of feather structure is excessive for insulatory purposes, but necessary for flight. Others have argued that the energy needed for flight requires the prior development of an insulating layer. Regal suggests that we should not assume that structures originated in adaptation to their ultimate functions, and reviews instead his theory that feathers began as heat shields that only later became further modified for both flight and insulation. His paper is a sensible and amusing essay on the limits of adaptational analysis and a reminder that animals are more versatile in their behavior than we often credit them to be.

These continuing disagreements suggest that the ability of functional morphologists to predict the behavior of animals on the basis of their structure is severely limited outside the use of analogies with living forms whose actions can be observed. There is no analog of *Archaeopteryx* alive today to serve as such a model, and one despairs that morphologists

will ever agree on the behavior of *Archaeopteryx* or its role in the origin of flight. Perhaps, despite the cleverness of the interpretations, the available evidence simply is not adequate to provide an understanding of the origin of flight in birds. This may have to await the discovery of additional fossil forms revealing new stages in the historical process.

A third problem is determining which group of reptiles gave rise to birds, and this is confounded by the question of the exact phylogenetic position of *Archaeopteryx*. The leading contenders are crocodilians, thecodonts, and theropods. The crocodilian theory is clearly in decline on the basis of recent anatomical studies. The once-popular thecodont theory still has adherents, but their position is eroded by the argument of Gauthier and Padian that thecodonts do not constitute a monophyletic group. They show that thecodonts merely are archosaurs that are not crocodiles, pterosaurs, dinosaurs, or birds, and that the origin of birds from "unknown thecodonts" is meaningless. Overall, the derivation of birds from theropods, as advocated by Ostrom, appears to be the dominant theory.

Many other topics are discussed in this book, including the classification, habitat, and anatomical structure of *Archaeopteryx* and the history of its discovery. Just as *Archaeopteryx* ends with an unusual caudal appendage, so does this book end with a bizarre tale. In a chapter written after the conference, Rietschel discusses the claim of astronomer and science-fiction writer Fred Hoyle that the feather impressions of *Archaeopteryx* are forgeries. The matter is effectively laid to rest, but one must wonder what damage to the credibility of science may result when the popular press reports such victories of arrogance over competence. Perhaps this is why the one point on which the conferees agreed unanimously was the declaration that "Organic evolution is a fundamental process of biology, and we recognize the importance of the *Archaeopteryx* contribution to that problem."—ROBERT J. RAIKOW.

PHYSIOLOGICAL STRATEGIES IN AVIAN BIOLOGY. By J. G. Phillips, P. J. Butler, and P. J. Sharp. Blackie and Son, Glasgow, Scotland, and Chapman and Hall, New York, New York, 1985:218 pp. $39.95 (cloth) $19.95 (paper).—". . . birds are endowed with easily studied morphological, behavioural and physiological adaptations which illustrate general principles of biological and practical importance. It is for this reason that birds are used as models in many areas of research . . . ." For an ornithology that has outgrown its descriptive texts, introductions to analytical ecology and physiology of birds are particularly welcome. This volume of the Tertiary Level Biology Series follows and frequently cites its predecessor, "Avian Ecology" by C. M. Perrins and T. R. Birkhead (1983).

The authors write with considerable expertise, among them having contributed significantly to the primary literature in most of the major divisions of avian physiology treated herein.

A brief review of avian respiration, circulation, and skeletal muscles precedes the analysis of flight energetics and physiology. Walking, running, swimming, and diving locomotion also are discussed. This is followed by a chapter on migration and orientation, which includes a brief but good section on energy conservation in flight.

The two following chapters discuss homeostatic regulation. Consideration of thermoregulation is equally divided between cold and heat stress responses. From torpor in poorwills and hummingbirds to circulatory strategies of raptors and heat exchanges of penguins, the examples chosen reflect more of the diversity of birds and environments than the other chapters.

The treatment of osmotic regulation includes behavioral aspects such as thirst, salt appetite, drinking, feeding strategies, and timing to avoid extreme stresses. The statement that ". . . a small bird with a high metabolic rate, thus producing relatively larger amounts

of free water, can tolerate a higher salinity of drinking water" overlooks the fact that respiration of the required oxygen results in sufficient evaporation to cancel the size-dependent rate of oxidation water production.

Salt glands have evolved in most marine and predatory birds, but not in the majority of bird species. Despite 11 pages of text that emphasize salt glands, twice as much as for kidney function and evaporation, there is no indication of the proportionate contribution of salt glands vs kidneys and gut to sodium and chloride excretion. Figure 5.4 on salt-gland structure lacks labels, unfortunately.

The topic of reproduction is divided into two chapters, one on reproductive system function and one on "The Environment and Reproduction." The latter is one of the most interesting chapters in the book. The concluding chapter goes into "applied aspects" of domestication and intensive farming and the consequences of pollution, particularly oil contamination, unfortunately made very relevant by news of the recent Port Angeles oil spill disaster.

An index is not crucial for a short reader, but this one is little more than an incomplete listing of bird species. To find "shivering" look under "budgerigar," "torpor" under "hummingbird," "kidney" under "starling" or "Savannah Sparrow." For "diving," "receptors," "blood," "Fick principle," or any symbols, one must flip through the text. At least seven species discussed in the text lost common or scientific name, or were omitted.

"Strategy" is perhaps the number one buzz-word of contemporary ecology, an anthropomorphism that gives meaning to the ecologist's life, as teleologies do for the physiologist. The definition from "Webster's New Universal Unabridged Dictionary" that seems to apply for our use of "strategy" is "skill in managing or planning, especially by using a ['plan, scheme, artifice, trick']." I was initially excited by the title of this little book, hoping that it would further my own efforts of several years to "sell" physiology to ecologists. To succeed, the volume would have to go beyond description of mechanisms to show how birds solve specific problems with neat physiological tricks. Of course, no strategy can be implemented or understood without the mechanisms, so much of such a sales effort is an exercise in packaging. By the oversimplification of adding up the number of pages actually discussing how challenges are met or problems are solved, I find that about 13 per cent of the book is devoted to what might be billed as "strategies," less than the emphasis implied.

The book was written "for advanced undergraduates . . . also . . . for the informed amateur ornithologist," "designed to be self-contained and, as a result, to stand on its own . . . ." That needs to be qualified: the book is for the student who has already taken some physiology. Strain, breaking force, STPD, thermoneutral temperature, drag coefficient, substance P, enkephalin, cytosolic fraction, horseradish peroxidase, and ouabain are among the terms used without explanations or definitions for the uninitiated. Several allometric relations are given six pages before explaining the allometric relationship. Reference is made and an illustration devoted to Rayner's vortex theory of flight without telling how a vortex would propel a bird. On p. 20, hyperventilation is implied (without definition) to be ventilation above metabolic demands, but on p. 28 it occurs when the bird is acidotic, indicating inadequacy for metabolic demands. Ventilation volume and oxygen extraction are used without the basic conservation equation that would make their significance clear to the undergraduate. Names of central nervous system parts are mentioned without any visual image.

Editorial and typographical errors are relatively few. On p. 12, reference to Fig. 3.6 should be to 2.3; reference to 5.3.2 on p. 91 should be 5.5.3f; stroke volume was omitted from an equation on p. 22; turkeys are altricial and canaries precocial in Fig. 6.12 legend.

The oil glut has slowed our domestic inflation, but the price of imported books is still

upsetting. While enriching the curriculum, the two avian paperback tertiary readers, added to assigned traditional ornithology text and field guide, would make an expensive book list.

This is an informative review. With help, the undergraduate can use it. The book also would complement previous experience limited to mammalian or human physiology by comparative exposure to the physiology of an independently evolved, fascinating class of high-energy homeotherms.—WILLIAM A. CALDER, III.

BIRDS OF SOUTHERN AFRICA 1: KRUGER NATIONAL PARK. By Kenneth Newman. Macmillan. South African Publishers, Johannesburg, South Africa, 1980 (reprinted 1981):242 pp, 4 line drawings, 2 maps, 106 colored plates. $14.00.—The monumental six-volume works of C. W. Mackworth-Praed and Captain C. H. B. Grant, "African Handbook of Birds," were for many years the standard identification and reference guides for Africa's rich avifauna. Series two of these books, the two-volume "Birds of the Southern Third of Africa," served ornithologists in southern Africa from 10 degrees south latitude to the Cape. Recently several other excellent African field guides have been published. Kenneth Newman's books are among them.

"Birds of Southern Africa 1: Kruger National Park" is an attractive, compact, and well-organized guide of the park, which at 1,948,528 hectares is South Africa's major conservation area. The park is located in the Transvaal Lowveld, in the northeastern area of the country. No fewer than 480 species of birds have been recorded within its boundaries.

The format is convenient for field use: full color plates of paintings appear on the right hand page, and species descriptions and maps of their ranges within the park, when known, appear on the left hand page. No species measurements are included, but the paintings are scaled to size. The author has prepared all paintings and the text. Two pages of weaver-nest sketches are included. A major disadvantage of the guide is that 71 species that have been recorded within the park and are listed in the two appendixes, are neither described nor illustrated.

Newman's "Birds of Southern Africa," published in 1983, is a more comprehensive field guide that covers all of Africa south of the Cunene, Okavango, and Zambesi rivers. All species known to occur in this region are illustrated and described in this more recent book, including all species known to occur in Kruger National Park. For the bird student visiting or residing in Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland, or Zimbabwe, Newman's "Birds of Southern Africa" is more useful than "Birds of Southern Africa 1: Kruger National Park," and it is therefore recommended for general field use in a far wider area of southern Africa.—LARRY SCHWAB.

WILDFOWL. By Eric Hosking, text by Janet Kear, and foreword by Konrad Z. Lorenz. Facts on File, New York, New York, and Bicester, England, 1985:153 pp., numerous color and black-and-white photographs. $24.95.—This volume is intended to showcase the work of well-known British bird photographer Eric Hosking. The text, by Janet Kear, presents a popular overview of waterfowl throughout the world, in seven chapters, covering such areas as evolution, courtship, nest and eggs, parental care, and flight and migration. Hosking's photographs are intended to illustrate the subject matter of each chapter.

What could have been a visual treat is, unfortunately, visually annoying. Printed in Singapore, the color plates are very grainy, and many are also somewhat off register in appearance. Others are badly out of focus, perhaps in some cases due to excessive enlargement in an attempt to illustrate a special courtship posture or some other behavioral con-

sideration. (The relatively few black and white photographs are uniformly sharp.) The text itself is accurate, well written, and covers a remarkable diversity of subject matter in a concise style. In contrast to the color photographs, however, Kear's writing is at times too crisp, often leaving the reader wishing for more details. A useful addition to the end of each chapter would have been a list of suggestions for further reading, or at least a section of major references at the end of the book would have been helpful; no such information is provided. "Wildfowl" is dedicated to England's noted conservationist Sir Peter Scott. The intent was good, but the poor quality of photographic reproduction renders the book disappointing and not worth the price. This certainly does not represent Hosking at his best.—ROBERT C. LEBERMAN.

BIRD ETCHINGS: THE ILLUSTRATORS AND THEIR BOOKS, 1655–1855. By Christine E. Jackson. Cornell Univ. Press, Ithaca, New York, 1985:292 pp., 4 colored and 79 uncolored plates. $55.00.—Most of the recent spate of books on bird art, whether on the work of a single artist or of a genre, have tended to be of the coffee-table ilk, designed to appeal more to the eye than to the intellect (even though the text may sometimes be genuinely authoritative). This generic designation by no means applies to Christine Jackson's latest scholarly book (she is also the author of "Bird Illustrators: Some Artists in Early Lithography" [Witherby, London, England, 1975], which, although adorned with 14 colored plates, is equally scholarly.) Ms. Jackson is identified on the jacket of her new book as a former college librarian and "an amateur naturalist in the same tradition as the people she writes about in *Bird Etchings.*" These two aspects of her life are precisely reflected in her text. She is obviously professionally familiar with the world of books and printing, and her research into the lives of authors and illustrators of early ornithological works appears to have been thorough (this book was already mentioned as being "in preparation" on the jacket of her 1975 book) and nearly impeccable.

On the other hand, Jackson's *ornithology* is what we might expect of the keen but somewhat provincial British amateur naturalist. Her nomenclature of non-British birds, both scientific and English, is often neither up-to-date nor accurate; her authorities were the 5th (1957) edition of the A.O.U. "Check-list" (which she misspells as "checklist") for "North American and Nearctic species [*sic*]," and Gruson's 1976 "Checklist of the World's Birds" (which she cited as "Checklist of the Birds of the World"). Her problems with nomenclature are exemplified by the caption to Plate 19: "Mark Catesby's plate depicting the blue jay, now the crested jay (*Cyanocitta cristata*); Plate 15 of *Natural History of Carolina.*" Catesby's plate is clearly labeled "The crested jay"; Jackson got the chronology of the English names backward. A more extreme example of Jackson's ornithological naïveté is the caption to Plate 7, on which is reproduced a drawing by William Swainson from his monograph "Flycatchers" (Jardine's Naturalist's Libary, Ornithology, Vol. 10, Plate 22, 1838). This portrays a female *Platysteira cyanea,* an African monarchine for which (at least) the names Wattle-eyed Flycatcher, Common Wattle-eye, Brown-throated Wattle-eye, and Scarlet-spectacled Wattle-eye are used in recent world lists and African field guides (Gruson calls it just "Wattle-eye"). Swainson's plate, however, is lettered "spectacle tody"; Jackson took that name literally, looked up the distribution of todies, and consequently attributed *Platysteira cyanea* to the West Indies! On p. 111 she correctly associates the British name "great white heron" and the scientific name *Egretta alba,* but then goes on to state that "the American form is the common egret, *Casmerodius albus.*" She obviously meant that this was the American *name usage,* not realizing that the word "form" would imply a *taxon* to many readers. On p. 115 she gives the English name of *Otus asio* as "red owl" and misidentifies the "Bastard Baltimore

of Catesby i.49" as "now the northern oriole, *Icterus galbula*" (it is, in fact, the Orchard Oriole, *I. spurius*). No sex is given in the original caption by George Graves for his Red-breasted Merganser (*Mergus serrator*) reproduced here as Plate 61; Jackson erroneously calls it a female. Several additional problems with the identification or nomenclature of birds could be cited.

But this isn't really a "bird book," and in the context of Jackson's biographic, bibliographic, and iconographic research, the errors listed above are relatively unimportant. I don't know enough about most of the artists discussed in this book to detect errors of fact or interpretation as easily as I could the ornithological errors. I noted only two during my reading of the entire book. On pp. 92–93, Jackson states that George Edwards "resolved not to part with any colored or uncolored prints while he was alive in case unskilled colorers should work on them and spoil them." This just doesn't make sense, and consultation of Vol. 1, p. xx of Edwards' "A Natural History of Uncommon Birds . . ." (1743) reveals that, as one might expect, Jackson's words ". . . colored or . . ." should be deleted. On p. 231 she reports as fact Audubon's oft-repeated tall tale that he had studied art with the famous French painter Jacques-Louis David (see Harwood and Durant, Audubon 87[3]:58–118, 1985).

With errors thus disposed of, what does Jackson's book have to offer? The bulk of her text is devoted to biographies of 16 author-artists of early ornithological works, many of whom will be unfamiliar to most American readers: Francis Willughby (1635–1672), John Ray (1627–1705), Eleazar Albin (d. 1741/42), Mark Catesby (1683–1749), George Edwards (1694–1773), Thomas Pennant (1726–1798), William Hayes (1735–1802), John Latham (1740–1837), John Walcott (1754/55–1831), William Lewin (1747–1795), James Bolton (d. 1799), Edward Donovan (1768–1837), George Graves (b. 1784), Prideaux John Selby (1788–1867), Sir William Jardine (1800–1874), and John James Laforest Audubon (1785–1851). Jackson has been, in my opinion, highly successful in giving the reader a "feel" for the times and the places (mostly England) in which these men lived. The continuing improvements in ornithological knowledge, in style and accuracy of depiction of birds, and in methods of reproducing illustrations, are all faithfully described. One is inevitably left with a sense of admiration for the perseverance of these pioneers, especially those without great inherited wealth. Many contemporaries of the biographees are mentioned, including especially those who contributed their artistic or technical talents to the production of the listed ornithological works, and those who supplied living or preserved birds as models for the artists.

The title of the book is misleadingly restrictive. Although Jackson carefully distinguishes the techniques of etching and engraving, both in her introductory pages and in an appendix, many of the featured ornithological works were illustrated with engravings rather than etchings.

The book closes with several appendices and indices: "Continental Illustrated Bird Books Published to 1660"; "The Use of Metal for Bird Illustrations," a useful explanation of the principal techniques ("etch" is from the Dutch word *etsen,* "to bite away"); "The Main Periodicals with Engraved/Etched Bird Illustrations" (of 6 listed, published between 1790 and 1853, 3 were not "periodicals" in the sense that we generally use this word, but *books* that appeared in parts); "Editions, Impressions, and Special Issues" (clarifying the reasons for the many variations seen in extant copies of these books); "Notes" to each of the chapters, giving sources in abbreviated form; "Selected Bibliography and Chapter Sources" with full citations; "Name Index" (i.e., people and institutions), and "Index of Avifaunal Species" (i.e., scientific names of birds).

Although this review does begin with traditional nit-picking, I must close by emphasizing that I thoroughly enjoyed reading "Bird Etchings," I learned a lot, and I highly recommend it to anyone interested in the history of ornithological art and literature.—KENNETH C. PARKES.

THE WILDLIFE GARDENER. By John V. Dennis, illus. by Matthew Kalmenoff. Alfred A. Knopf, New York, New York, 1985:293 pp., 65 drawings. $17.95.—John V. Dennis, author of "A Complete Guide to Bird Feeding" and "Beyond the Bird Feeder," explains how to create and enjoy a wildlife garden in his latest book. His purpose is to encourage many to start wildlife gardens, believing that the more such minihabitats there are, the better it is for the wildlife he wants to help, and that even small gardens, suitably planted for wildlife, help take the place of lost natural habitat. In fact, Dennis argues that such a garden can support a larger and more diverse wildlife community than a similar area of natural habitat. His book is written for the general reader, one with at least some land to plant and an affinity for wildlife.

"The Wildlife Gardener" differs from many books that emphasize attracting birds. Dennis encourages one to improve a yard's attractiveness to all kinds of wildlife by using plantings that provide shelter and food, arguing that all manner of living things add to our enjoyment of suburban and rural life. He encourages us to enjoy a larger variety of animals. He includes chapters on plantings, use of ponds, pools and other sources of water, food plants for birds, nesting sites for birds, hummingbirds, and mammals. There are four chapters devoted to attracting insects: bees, butterflies, moths, and other insects. Other chapters cover earthworms, reptiles, and amphibians. The excellent appendix supplies an annotated list of small trees, shrubs, vines, and flowers useful as food or shelter for wildlife. There is a bibliography and index.

The best thing about this book is the hundreds of interesting and useful hints, recommendations, and facts. For example, there is a list showing insect pests and their insect enemies. Dennis recommends setting aside a remote corner of the yard, if it can be spared, to grow weeds to attract butterflies and other insects. He has counted 38 species of butterflies coming to dogbane (*Apocynum* sp.). Many plants he recommends are plants we consider to be weeds, but are used as garden plants in Europe (i.e., sumacs [*Rhus* spp.] and goldenrods [*Solidago* spp.]).

Birds are not neglected. Ideas, such as providing mud for nesting material, and the use of dripping water and other sources of water, in addition to the standard bird bath, will increase the variety of species using the garden. Trees and shrubs are analyzed for their usefulness as nesting sites and are grouped according to how many species have been observed to nest in each kind. The emphasis is on garden and landscaping, not bird houses and feeders.

Some of the mammals Dennis discusses, opossums, moles, bats, raccoons, woodchucks, and rabbits for example, are generally thought of as pests. He stresses methods for controlling wildlife damage and discusses the ecology and beneficial aspects of each. Yet some readers will balk at inviting some kinds of animals into the yard by offering dog food, fruit, and vegetables; and neighbors, whose gardens are raided or fruit trees girdled, may not understand one's wildlife zeal. The serious wildlife gardener will have to show neighbors how to control damage and do some diplomatic education in ecology and conservation. Gardeners who enjoy wildlife are certain to find this book useful and entertaining. Anyone interested in wildlife, especially the food habits of common animals, will find "The Wildlife Gardener" appealing.—ALBERT R. BUCKELEW JR.

AUSTRALIAN BIRD CALLS, 2nd Edition. By John N. Hutchinson. Series 1, Western Australia. No publication date given. Compact Cassette (approx. 30 min/side). Monaural. Published privately by the author and available from him at Wildlife Sound Studios, Balingup 6253, Western Australia. $10.00 Australian currency.—This well-produced recording treats the typical songs and calls of 50 bird species of western Australia. The recordings were made in the period 1962–1969, mostly by Hutchinson, primarily in natural "bush settings,"

although three were of captive birds—Whistling Eagle (*Haliastur sphenurus*), White-tailed Cockatoo (*Calyptorhynchus baudinii*), and Cockatiel (*Nymphicus hollandicus*). Narration is confined to an announcement of each species just before it is heard, by Miss Gillian Waite, a lady with a pleasant voice. The cardboard insert has a color photograph of a logrunner, the Wedgebill (*Sphenostoma cristatum*). On the back of the insert there is a brief paragraph about the recordings (made using an open microphone with no parabola). There also is information that the sounds are available on a 12-inch LP disc and that Series 2 and 3 are available. A folded sheet of paper contains a list of the 50 species by common name, scientific name, general recording locality, and remarks (such as "warning call when lizard entered nest tunnel. Song."). The presentation is in a systematic order, beginning with an Emu (*Dromaius novaehollandiae*), followed by a Yellow-nosed Albatross (*Diomedea chlororhynchus*) and then continuing with an ibis, the Whistling Eagle, 1 stone-curlew, 2 doves, 5 parrots, 2 cuckoos, 1 owl, 1 kookaburra, 1 bee-eater, the Noisy Scrub Bird (*Atrichornis clamosus*), 1 lark, 1 babbler, 3 warblers, 8 flycatchers, the logrunner, 1 Australian nuthatch, 2 flowerpeckers, 8 honeyeaters, 1 waxbill, 1 magpie-lark, 2 wood-swallows, 1 butcherbird, 2 bowerbirds, and 1 crow. The recordings are uniformly very good, although many are not much fun to listen to just for their sonic characteristics. Ths is an important publication of reference material, which together with the other two in the series (I have no information about them) should certainly comprise a useful introduction to Australian bird sounds for amateur and professional alike.—JOHN WILLIAM HARDY.

## APPLICATION TO THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following application has been received by the Commission and has been published in Vol. 43(2) of the *Bulletin of Zoological Nomenclature* (9 July 1986). Comment or advice is welcomed and should be sent % British Museum (Natural History), London, England. Comment will be published in the *Bulletin*. P. K. Tubbs, Executive Secretary.

Case No. 1051—*Bubo* Dumeril, 1806 and *Surnia* Dumeril, 1806 (Aves): proposed confirmation on the Official List.

## SOUTH AFRICAN ORNITHOLOGICAL SOCIETY SYMPOSIUM

Birds of evergreen forest will be the subject of a symposium to be held 8–10 September 1987 at The Wilderness, Cape Province, South Africa. Papers and posters on forest bird communities, biogeography of forest birds, and conservation of forest avifaunas are solicited. Contact the Symposium Organising Committee, E.C.W.B.S., P.O. Box 1305, Port Elizabeth, 6000, South Africa for details.

*Wilson Bull.*, 98(4), 1986, pp. 626–638

# PROCEEDINGS OF THE SIXTY-SEVENTH ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Sixty-seventh Annual Meeting of the Wilson Ornithological Society was held Thursday, 17 April to Sunday, 20 April 1986 at the Holiday Inn in Gatlinburg, Tennessee in joint session with the Tennessee Ornithological Society. The meeting was sponsored by the Knoxville Chapter of the Tennessee Ornithological Society. Charles P. Nicholson chaired the Local Committee on Arrangements, while Audrey R. Hoff served as treasurer. The committee members were Fred J. Alsop, III, James M. Campbell, Betty Reid Campbell, Marcia L. Davis, Barbara Finney, Linda J. Fowler, Louise F. Fuller, Ron D. Hoff, James A. Tanner, and Nancy Tanner.

The Council met from 13:00 to 18:00 on Thursday, 17 April. Registration for the 157 guests and members began that evening, followed by a reception in the Magnolia Suite. The opening session was held in the Greenbrier Room where the societies were welcomed by Stan Cantor, Chief of Visitors' Services for the Great Smoky Mountains National Park. President Clait Braun responded for the Wilson Ornithological Society and Jim Ferguson responded for the Tennessee Ornithological Society. The scientific papers presentations were made daily, with double sessions necessary on the first day. Of particular significance was the symposium on the Birds of the Southern Appalachians chaired by Dr. George A. Hall on Saturday afternoon. A presentation made on Friday evening by John Peine of the Great Smoky Mountains National Park provided an overview of the scientific programs being conducted in the park.

Early morning field trips were scheduled on both Friday and Saturday with the option of walking to Mynatt Park, directly adjacent to the Holiday Inn, or carpooling to the area around the Sugarlands Visitors Center in GSMNP. These tours were ably led by Jim Campbell and Fred Alsop of the local committee. A wildflower tour was scheduled Friday afternoon as part of the spouse's program, but attracted a number of members as well. On Sunday, extended field trips were made to various sites throughout the Great Smoky Mountains National Park.

The annual banquet was held in the Greenbrier Room Saturday evening. The following awards were presented:

EDWARDS PRIZE (for the best major article in volume 97 of *The Wilson Bulletin*)

Frances Hamerstrom, Frederick N. Hamerstrom, and Charles J. Burke, "Effect of voles on mating systems in a central Wisconsin population of harriers," Wilson Bull. 97:332–346.

LOUIS AGASSIZ FUERTES AWARDS

John A. Gerwin, "The evolution of hummingbirds (*Heliodoxa*): a molecular phylogeny."
Paul Hendricks, "Evolution of monogamy in Aleutian Rosy Finches."

PAUL A. STEWART AWARDS

J. M. Black, "Breeding biology of Barnacle Geese."
J. A. Clarke, "White-tailed Ptarmigan in the Sierra Nevada Mountains: a comparative study of an introduced population."
D. Gawlik, "A field study of the distribution, abundance, and reproductive success of Loggerhead Shrikes in South Carolina."
C. A. Haas, "Site fidelity and dispersal in a patchy environment."
A. R. Hanson, "Black Duck renesting in relation to interspecific pair formation between Black Ducks and Mallards."
G. E. Hill, "The reproductive consequences of subadult plumage in male Black-headed Grosbeaks."
P. M. Mayer, "Population ecology of the Piping Plover in the northern Great Plains."
H. B. Suthers, "Pesticide residues and death in backyard songbirds."
R. C. Wright, "Assessing blackbird damage to ripening rice in Matagorda County, Texas."

ALEXANDER WILSON PRIZE (for best student paper at the meeting, selection committee chaired by Mitchell Byrd)

David F. Westneat, University of North Carolina–Chapel Hill, "Extra-pair fertilizations in the Indigo Bunting."

There was no Margaret Morse Nice Award presented this year. Professor James A. Tanner gave a most fitting address to end the banquet festivities.

## FIRST BUSINESS MEETING

The first business meeting was called to order by President Braun at 09:05, Friday, 18 April in the Greenbrier Room of the Holiday Inn–Gatlinburg. The names of those appointed to the auditing committee were announced. Secretary Zimmerman summarized the highlights of Thursday's Council meeting, reporting that Keith Bildstein had been reelected as editor but that a new editor will be needed for the Bulletin effective with Volume 100. It is also contemplated that membership dues will need to be increased in 1988. Of special import in regards to the centennial meeting in 1988, it was announced that the members of the Executive Council had each pledged $100 to facilitate our reaching a goal of $5000 for the Centennial Fund. Lastly, Zimmerman asked those attending to stand to honor those members who had died since we last met together—Rudyerd Boulton (Salisbury, Zimbabwe), Eugene M. Heitzman (Pilat Point, Texas), Edgar B. Kincade (Austin, Texas), Cyrus Mark (Glencoe, Illinois), E. P. Richardson (Philadelphia, Pennsylvania), and Robert H. Stabler (Colorado Springs, Colorado).

David Pitts, chairman of the Nominating Committee, offered the following slate for consideration by the membership: President—Clait Braun, First Vice-President—Mary Clench, Second Vice-President—Jon Barlow, Secretary—John Zimmerman, Treasurer—Bob Burns, Elected Council Member for 1987–89—Richard Conner.

Robert D. Burns then gave the treasurer's report.

# REPORT OF THE TREASURER
## 1 January 1985 to 31 December 1985

*GENERAL FUNDS*

| | | |
|---|---|---|
| *RECEIPTS* | | |
| Dues collected in 1985 | | |
| Regular and Sustaining Memberships for 1985 | $ 10,350.00 | |
| For 1986 | 14,887.50 | |
| Student Memberships for 1985 | 1,578.00 | |
| For 1986 | 1,175.00 | |
| Family Memberships for 1985 | 200.00 | |
| For 1986 | 340.00 | |
| TOTAL DUES | | $ 28,530.50 |
| Subscriptions to *The Wilson Bulletin* | | |
| For 1985 | $ 9,883.00 | |
| For 1986 | 3,632.50 | |
| TOTAL SUBSCRIPTIONS | | $ 13,515.50 |
| Back issues of *The Wilson Bulletin* | | $ 882.00 |
| Interest and Dividends | | $ 21,806.58 |
| Royalties | | $ 1,927.00 |
| Contributions from Authors | | $ 4,867.26 |
| Contributions to The Van Tyne Library | | $ 116.00 |
| Contributions to the Student Membership Endowment | | $ 555.00 |
| Contributions to General Endowment (Life Members and Patrons) | | $ 5,687.00 |
| Contributions to the Sutton Art Prize | | $ 500.00 |
| Contributions to the Edwards Prize | | $ 500.00 |
| Contributions to the Wilson Prize Endowment | | $ 123.00 |
| Contributions to the Centennial Fund | | $ 70.00 |
| Fund from the Green Bay, Wisconsin Meeting | | $ 500.00 |
| Fund from the Fort Collins, Colorado Meeting | | $ 835.61 |
| TOTAL RECEIPTS | | $ 80,415.45 |
| *DISBURSEMENTS* | | |
| *The Wilson Bulletin* | | |
| December 1984 | $ 18,775.98 | |
| March 1985 | 11,295.92 | |
| June 1985 | 10,264.80 | |
| September 1985 | 11,849.77 | |
| Colorplates | 3,737.88 | |
| Editorial Expenses | 2,363.80 | |
| Travel | 414.65 | |
| TOTAL PRODUCTION COSTS | | $ 58,702.80 |
| OSNA Expenses (including Newsletter) | | $ 15,602.15 |
| Student Awards | | $ 3,050.00 |
| Dues to International Council for Bird Preservation 1985 | | $ 100.00 |
| Treasurer, Postage and Bond | | $ 139.00 |
| Student Award Notice Printing | | $ 61.60 |
| Meeting Announcements for Colorado Annual Meeting | | $ 1,432.16 |
| Cash Advance to Local Committee for Gatlinburg Meeting | | $ 1,000.00 |

| | |
|---|---|
| Sutton Art Prize | $ 500.00 |
| Postage for return of Sutton Art Exhibit | $ 25.68 |
| Subscription Refunds | $ 66.00 |
| Printing and Mailing of Back Issues | $ 622.05 |
| Incorporation Fee for 1984 and 1985 | $ 47.00 |
| Scottish Historical Society for Wilson Gravesite | $ 200.00 |
| Deposit of Life Membership, Patron and Endowment Contributions | $ 5,371.00 |
| TOTAL DISBURSEMENTS—1 January 1985 to 31 December 1985 | $ 86,919.44 |
| 1985 DEFICIT | $ 6,503.99 |

*CASH ACCOUNTS*

| | | |
|---|---|---|
| Checking Account, Peoples Bank, Gambier, Ohio 31 December 1985 | $ 3,480.55 | |
| Savings Account, 31 December 1985 | 224.41 | |
| Dreyfus Liquid Assets | 31,161.66 | |
| TOTAL CASH ON HAND | | $ 34,866.62 |

*DESIGNATED ACCOUNTS*

LOUIS AGASSIZ FUERTES RESEARCH FUND

| | |
|---|---|
| RECEIPTS | |
| Endowment Earnings | $ 600.00 |
| DISBURSEMENTS | |
| Gloria R. Dobush | $ 300.00 |
| John M. Marzluff | $ 300.00 |

ALEXANDER WILSON PRIZE

| | |
|---|---|
| RECEIPTS | |
| Endowment Earnings | $ 200.00 |
| DISBURSEMENTS | |
| Andrew Balestracci | $ 200.00 |

ERNEST P. EDWARDS PRIZE

| | |
|---|---|
| RECEIPTS | |
| E. P. Edwards | $ 500.00 |
| DISBURSEMENTS | |
| J. M. Sprinkle | $ 175.00 |
| C. R. Blem | 175.00 |
| Peter Fetterolf | 150.00 |

PAUL A. STEWART AWARDS

| | |
|---|---|
| RECEIPTS | |
| Endowment Earnings | $ 1,650.00 |
| DISBURSEMENTS | |
| Frank J. Joyce | $ 275.00 |
| Mark J. Kasprzyk | 275.00 |
| Laurie H. MacIvor | 275.00 |
| Wendy M. Jackson | 275.00 |
| Carola A. Haas | 275.00 |
| Geoffrey E. Hill | 275.00 |

### Annual Meeting Reserve Fund

| | |
|---|---|
| RECEIPTS | |
| Refunds from the 1983 and 1985 Meetings | $ 1,335.61 |
| 1984 Balance | (96.83) |
| DISBURSEMENTS | |
| 1985 Meeting | $ 1,432.16 |
| 1986 Meeting (Cash advance) | 1,000.00 |
| 1985 Balance | (1,193.38) |

### Endowment

| | |
|---|---|
| Value of Endowment Fund, 31 December 1984, at cost | $196,726.20 |
| Transfer of Awards Endowment Funds in the Dreyfus Liquid Assets Account | $ 17,622.00 |
| Life Membership and Patron Payments | 5,371.00 |
| Capital Gains on Securities Sold | 11,225.57 |
| Value of Endowment Fund 31 December 1985, at cost | $230,984.77 |

### Individual Endowment Accounts of The Wilson Ornithological Society

| | |
|---|---|
| Fuertes & Nice Awards | $ 10,000.00 |
| Stewart Awards | 23,316.00 |
| Edwards Award | 1,300.32 |
| Wilson Prize | 1,654.00 |
| Student Membership | 555.00 |
| Colorplate Fund (approx.) | 30,000.00 |
| General Endowment | 164,159.45 |

The Editor's report was presented by Keith L. Bildstein.

## EDITOR'S REPORT—1985

In 1985 167 manuscripts (67 papers, 100 notes) were submitted to my office. This is a 24% increase over the number submitted in 1984. As of late April 1985, 45% of these manuscripts have been accepted, 30% have been rejected, 2% have been withdrawn, 19% have been returned to authors for revision, and 4% are under review. Based on these numbers, I project 1985 acceptance rates of 55% for manuscripts submitted as major papers and 55–60% for manuscripts submitted as general notes. Major papers received in 1985 were returned to the author within 84 ± 37 days [SD] of receipt. General notes were returned within 78 ± 48 days of receipt. The "average" accepted ms was published within 10–11 months of receipt. All issues since June 1985 have been published on time. There are plans for color plates for all issues in 1986, as well as for the March and June issues of 1987.

The format of the *Bulletin* has been changed as of the March 1986 issue: (1) Abstracts have replaced summaries in major papers. (2) Author's addresses now appear as footnotes on the first page of major papers. (3) General Notes with more than 4 references have terminal literature cited sections. (4) Dates of reception as well as acceptance now appear in every ms.

Over the past year I have received essential assistance from many people in the Editorial Office and elsewhere. I thank the staff of the Allen Press, especially Arly Allen, Ken Blair, John Breithaupt, Guy Dresser, and Sharon Kendall. I also thank the members of the ad hoc Publications Committee, R. Banks, C. Braun, and F. Knopf, for their help. Others that I thank for their outstanding service include: Associate Editors, M. W. Collopy, R. N. Conner,

J. P. Myers, W. M. Shields, and J. R. Walters; Assistant Editors, A. E. Conway, J. A. Hovis, J. W. Johnston, J. B. Olson, D. L. Rankin, D. Gawlik, and A. Wenner; Review Editor George A. Hall; Color Plate Editor W. A. Lunk; Index Editor K. G. Beal; numerous members of the WOS, including C. Braun, S. Gaunt, A. Gaunt, J. Barlow, J. Jackson, and B. Burns; the 190 volunteer referees who reviewed mss for the *Bulletin* during the past 11 months; and Department of Biology secretaries E. Hill and S. Strait.

Keith L. Bildstein, *Editor*

Judy McIntyre, local chairperson for the 27–31 May 1987 meeting in Utica, New York hosted by Utica College of Syracuse University and the Kirkland Bird Club, ended the first business meeting with an illustrated invitation for next year.

## SECOND BUSINESS MEETING

President Braun called the second business meeting to order at 13:30 on Saturday, 19 April. The report of the Auditing Committee was received. Chairman Klamm presented the report of the Auditing Committee:

We, the undersigned, have reviewed the records presented by the treasurer covering the period of 1 January 1985 to 31 December 1985 with the intent of verifying that the records correctly reflect the assets of the Society along with the correct and timely posting of income and expenditures during this period. We found no errors and are satisfied that the financial report as presented correctly reflects the financial health of the Society. Further, we commend Dr. Robert Burns, treasurer, for his excellent work in fulfilling the responsibilities of his office for the year 1985.

William A. Klamm, *Chairman*
Herbert P. Zernickow
Harold Ratcliff
Robert A. Whiting

A motion to accept the report of the Auditing Committee was made by Jerry Jackson and seconded by Robert Whiting and passed by the assembled membership.

The Report of the Nominating Committee was recalled to the floor by President Braun and opened for further nominations. In a series of motions by Dick Stiehl and Helmut Mueller, Phillips Street and Jerry Jackson, William Klamm and Mary Clench, Sandy Gaunt and Helen Lapham, Mary Clench and Sandy Gaunt, and Dick Stiehl and Jerry Jackson and passed by the membership, the nominations for each office were closed without further additions and the slate was elected as presented by the Nominating Committee.

A motion by Mary Clench and seconded by Helen Lapham to accept the new members of The Wilson Ornithological Society by election was made and passed.

Elliott Tramer presented the report of the Resolutions Committee.

## REPORT OF THE RESOLUTIONS COMMITTEE

RECOGNIZING, that Great Smoky Mountains National Park (GSMNP) was established to protect one of the world's finest examples of temperate forests, and

RECOGNIZING, that GSMNP has been designated an International Biosphere Preserve in recognition of the uniqueness of its vegetation, and

RECOGNIZING, that the welfare of the animal life, including birds, of GSMNP depends on the welfare of its vegetation, and

WHEREAS, GSMNP is experiencing elevated levels of acid precipitation, acid fog, and atmospheric ozone, and

WHEREAS, an increasing body of scientific evidence has demonstrated the deleterious effects of these atmospheric changes on plant communities, not only in GSMNP but also elsewhere in the eastern United States and Canada,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its encouragement of the efforts of the Science Division of GSMNP to better document and understand the effects of air pollutants on the park's vegetation, and

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society strongly urges all responsible agencies to work vigorously to develop the legal and technical means for reducing the levels of atmospheric acids and ozone that now threaten our forests.

Clait Braun moved and Nancy Mueller seconded to accept this resolution. The motion passed.

WHEREAS, The Wilson Ornithological Society and the Tennessee Ornithological Society held a joint meeting from 17 to 20 April 1986 at Gatlinburg, Tennessee, sponsored by the Knoxville Chapter of the Tennessee Ornithological Society, and

WHEREAS, the local committee, chaired by Dr. Charles P. Nicholson, arranged varied activities, including superb accommodations, food and drink, evening programs and field trips, and

WHEREAS, the scientific program committee, chaired by Dr. Jon C. Barlow, assembled an impressive array of stimulating scientific papers, including a symposium on the birds of the southern Appalachians convened by Dr. George A. Hall,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society extends its sincere appreciation to all those organizations and individuals who worked so diligently to make this meeting a resounding success.

Robert Burns moved and Jerry Jackson seconded to accept this resolution, which then passed.

A motion for adjournment was made by Mary Clench and seconded by Sandy Gaunt.

The reports of the standing committees were given as follows:

## REPORT OF THE COMMITTEE ON STUDENT MEMBERSHIP—1985

A total of 230 letters was sent to selected members of the Wilson Ornithological Society who were in positions that afforded the identification of students eligible for the Student Membership Awards provided by the society. In addition to a set of application materials, a form was provided on which members could list the names of students who were not being nominated for an award but who should be sent information regarding student membership in the society. Announcements of the availability of these awards were also made in the Wilson Bulletin and in the Ornithological Newsletter. Application materials were sent in response to 10 letters of inquiry that were probably generated by these announcements.

Completed applications were received from 29 nominees. Members also provided the names of 17 students to whom an invitation to join the society was sent. As in the past, two criteria were used by the committee in the evaluation: (1) the applicant's demonstrated commitment to ornithology, and (2) the expectation for a long-term professional involvement in ornithology. The materials of the candidates were evaluated independently by the four members of the committee according to the following rating scale: 1—highly meritorious, top priority should be given to this student, 2—deserving, but definitely at a level below my highest rank, 3—marginally acceptable, but the giving of the award might facilitate their development, 4—not acceptable.

As the number of awards this year was not limited by a set amount of money "in the account," it was decided that successful candidates would have to obtain an average rating

between 1 and 2.4 on the above scale. Twenty-six candidates qualified; their names and schools are listed as follows: Michael E. Barnes, Kansas State Univ.; Constance J. Boardman, California State Univ.; Stephen C. Brown, Univ. Michigan; David A. Buehler, Virginia Tech; Linda A. Caine, Univ. Florida; John P. Carroll, Univ. North Dakota; Greg H. Farley, Kansas State Univ.; Thomas P. Fitch, Idaho State Univ.; Fernando G. Garcia, Programa Fauna de Mexico; Nicholas W. Gard, Macdonald College, Quebec; Dale E. Gawlik, Winthrop College; Michael T. Green, Univ. North Carolina; Floyd E. Hayes, Univ. Michigan; Gloria E. Jacoby, Univ. Kentucky; Paula K. Kleintjes, California Polytechnic State Univ.; Michael J. Kolasa, Northern Michigan Univ.; Natasha B. Kotliar, Univ. New Mexico; Keven J. Kritz, Univ. Missouri; Darrell E. Land, Univ. Florida; Michael P. Losito, Auburn Univ.; Craig D. Olawsky, Texas Tech Univ.; James C. Ozier, Univ. Georgia; Bradley E. Sample, Univ. Delaware; Birgit C. Schultz, McGill Univ., Quebec; Dave Shutler, Macdonald College, Quebec; Alexander P. Smith, Univ. North Carolina.

It was gratifying that there were two undergraduates among those receiving Student Membership Awards. The three unsuccessful student award nominees were sent letters inviting them to join the society.

Thomas C. Grubb
Charles F. Leck
Roland R. Roth
Richard N. Conner, *Chairman*

## MEMBERSHIP COMMITTEE REPORT—1985

The total paid membership in the Society as of 12 March 1986 was 2613. During the period, 147 new members joined the Society and 240 persons failed to renew membership, for a decrease of 93 members from the report of 14 April 1985. The OSNA office handled the bulk of the new membership requests. No members requested the use of the display board. Using the 1985 *Flock* as a basis, I determined the membership category (regular, student, life, or patron) of the society by state or Canadian province or foreign country (excluding Canada). The *Flock* lists 2298 U.S. members with 235 from California, 145 from New York, and 116 from Texas. Of the 198 Canadian listings, 96 were from Ontario. Australia, Japan, and West Germany lead the foreign nations with 13, 12, and 11 respectively. A total of 2622 Wilson Ornithological Society members are listed in the 1985 *Flock*. I suggest the data be considered when the site of the annual meeting is discussed. I realize that many factors contribute to the location, but if high meeting attendance is desirable, then attention should be paid to the geographic distribution of the membership.

The Society experienced a 3.65% decrease in membership in the past 11 months for an annual 3.88% reduction. With this reduction, I suggest that WOS members who are also active members in state ornithological societies be identified and asked to interface with their respective state societies on behalf of WOS. They would serve to promote WOS within the state societies and request flyers and a display board for their state meetings. Advertisements could also be designed for state journals (*Raven, Passenger Pigeon,* etc.), as well as more regional and national journals (*Western Bird Bander, J. Field Ornithol.*) and also perhaps for the National Audubon Society. I suspect that the advertisements in the state and regional journals would be inexpensive . . . perhaps free. Any advertisement in *Audubon Magazine* would cost, as would shipping the display board all around the country ($5.00/one way). If membership is a problem we as a Society wish to address, then it will require a commitment of a budget in the hundreds of dollars.

Richard Stiehl, *Chairman*

## LIBRARY COMMITTEE REPORT—1985

The Library functioned smoothly, and about at its usual level of activity, during the year 1985. We continue the long-standing relationship with the Bird Division of the University of Michigan Museum of Zoology, whereby (in return for convenient use of our collections by Museum personnel, students, and visitors) we enjoy excellent housing facilities as well as handling and clerical services. Janet Hinshaw, in fact, in her capacity as UMMZ Museum Technician, manages virtually all of our operations. The members of the Society, as usual, supported the Library generously and made good use of it, as indicated by the following statistics.

Total donations included 1235 items: 31 books, 209 journal issues, 49 reports, 12 newsletters, 933 reprints (750 of these from R. W. Storer), and 1 translation. These items were received from A. J. Berger, C. Brown, C. Chase III, J. Gapczynski, K. W. Haller, H. Harrison, J. Hinshaw, S. Holohan, J. Jehl, Jr., L. Kilham, H. Mayfield, R. D. Ohmart, R. B. Payne, S. Postupalsky, J. Renner, S. Richards, A. Richford (for Academic Press), C. Ross, P. Stettenheim, R. W. Storer, J. G. Strauch, Jr., M. Wolf (for Österreichische Gesellschaft für Vogelkunde), and Col. L. R. Wolfe: 23 members in all.

Items sold to augment the New Book Fund were 30 duplicate books (for $277) and 127 duplicate journal issues ($200). Purchased were 24 books, indices, and other publications, and 1 record, for a total of $565.51.

We received 157 titles from 113 exchanges of *The Wilson Bulletin,* 37 titles through 27 gifts, and 11 titles through 7 subscriptions, for a total of 205 journals and other items currently being received.

Loans to 47 members and institutions added up to 75 separate transactions, and involved 284 books, translations, and photocopies.

Of special interest will be the appearance, in the not-too-distant future, of an extensive bibliography of available English translations of foreign literature, including those in the WOS collection. This bibliography, long in preparation by Doug Siegel-Causey and Janet Hinshaw, has now been submitted for publication.

William A. Lunk, *Chairman*

## CONSERVATION COMMITTEE REPORT—1985

We have decided to undertake two separate efforts. Each will demand some extensive, original synthesis by individuals within selected areas of expertise and has resulted in the formation of two subcommittees: (1) *Conservation of Riparian Communities.* This effort will define the riparian issue, relate its special concern to those interested in avian conservation, acknowledge the economic demands placed on these systems, summarize current agency policies and guidelines for riparian conservation, and conclude with a list of recommendations for the future followed by literature citations. The respective members are: Dr. Fritz L. Knopf, Chairperson, U.S. Fish and Wildlife Service—Colorado; Dr. R. Roy Johnson, U.S. National Park Service—Arizona; Mr. Terrell Rich, U.S. Bureau of Land Management—North Dakota; Dr. Fred B. Samson, U.S. Forest Service—Washington; and Dr. Robert C. Szaro, U.S. Forest Service—Arizona. (2) *Conservation of North American Rallids.* This subcommittee will examine the relationship of this group of birds to population and habitat management practices for waterfowl enhancement in North America. The information on effects of these management programs upon rallid populations is scant, and needs synthesis. Rare, endangered, and status-undetermined species often occur in the same marshes with game species and the effects of hunting upon nongame species have not been identified as an issue. We intend to identify these issues and summarize information avail-

able, while providing guidance for future management and conservation efforts and research on the Rallidae. Members of this subcommittee are: Dr. William R. Eddleman, University of Wyoming; Dr. Fritz L. Knopf, Chairperson, U.S. Fish and Wildlife Service—Colorado; Mr. Brooke Meanley, Retired—Virginia; Dr. S. Dillon Ripley, Smithsonian Institution; Mr. Richard Zemball, U.S. Fish and Wildlife Service—California. Participants on both subcommittees are all members of WOS. Final statements from these subcommittees will be available for the 1987 meeting.

Fritz L. Knopf, *Chairman*

## PAPERS SESSIONS

Michael T. Green, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, and Jon H. Miller, P.O. Box 29, Lee Vining, CA, "Water Pipits (*Anthus spinoletta*) in the Sierra: origin and distribution of a recent invader."

Jon C. Barlow, Dept. Ornithology, Royal Ontario Museum, Toronto, ONT, W. Bruce McGillivray, Dept. Ornithology, Provincial Museum of Alberta, Edmonton, ALB, and Vincent L. St. Louis, Dept. Zoology, Univ. Toronto, Toronto, ONT, "The Warbling Vireo in Alberta—one species or two?"

Vincent L. St. Louis, Dept. Zoology, Univ. Toronto, Toronto, ONT, "Morphometric and genetic divergence among populations of the Eurasian Tree Sparrow (*Passer montanus*)."

J. D. Rising, Dept. Zoology, Univ. Toronto, Toronto, ONT, "Geographic variation in sex ratios and body size among wintering flocks of Savannah Sparrows (*Passerculus sandwichensis*)."

Sheila Conant, Dept. General Science, Univ. Hawaii, Honolulu, HI, "Morphological variation in two populations of Laysan Finches (*Telespyza cantans*)."

Jerome A. Jackson and Bette J. Schardien Jackson, Dept. Biological Sciences, Mississippi State Univ., Mississippi State, MS, "Countdown to extinction: can the Ivory-billed Woodpecker still exist?"

John L. Zimmerman, Div. Biology, Kansas State Univ., Manhattan, KS, "Territory selection and habitat in Henslow's Sparrows."

Petra Bohall Wood, Dept. Wildlife and Range Sciences, Univ. Florida, Gainesville, FL, "Abundance, habitat selection, and perch use of Loggerhead Shrikes in north-central Florida."

Doris J. Watt and Laura A. Sadowski, Dept. Biology, Saint Mary's College, Notre Dame, IN, "The development of courtship feeding in captive American Goldfinches."

Thomas A. Waite, Dept. Zoology, Ohio State Univ., Columbus, OH, "The effects of sociality and dominance on vigilance in Tufted Titmice."

R. N. Wiedemann and K. N. Rabenold, Purdue Univ., West Lafayette, IN, "The effects of social dominance between two subspecies of Dark-eyed Juncos (*Junco hyemalis*)."

Walter H. Piper, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, "Do dominant birds feed closer to cover than subordinates? Findings that contradict Schneider's distance hierarchy analysis."

Robert G. Hooper, USDA Forest Service, Charleston, SC, "Use of young longleaf pines for cavities by Red-cockaded Woodpeckers."

Thomas C. Edwards, Jr., Dept. Wildlife and Range Sciences, Univ. Florida, Gainesville, FL, "Nest tree characteristics of Ospreys (*Pandion haliaetus*) in north-central Florida."

Mark S. Woodrey, Dept. Zoology, Ohio State Univ., Columbus, OH, "Characteristics of Red-shouldered Hawk nests in southeast Ohio."

J. B. Grand and R. E. Mirarchi, Dept. Zoology-Entomology and Alabama Agric. Exper.

Sta., Auburn Univ., AL, "Habitat use by recently-fledged Mourning Doves (*Zenaida macroura*) in east-central Alabama."

John D. Thompson and Guy A. Baldassarre, Dept. Zoology-Entomology and Alabama Agric. Exper. Sta., Auburn Univ., AL, "Postbreeding habitat selection by resident Wood Ducks in north Alabama."

Tom Webber and Mary H. Clench, Florida State Museum, Univ. Florida, Gainesville, FL, "Body pterylosis and relationships of the vireos."

Mary H. Clench, Florida State Museum, Univ. Florida, Gainesville, FL, "Body pterylosis of the New Zealand Bush Wren: new information on the relationships of the Xenicidae."

John William Hardy, Florida State Museum, Univ. Florida, Gainesville, FL, and Dale J. Delaney, 155 15th St., No. 28, Del Mar, CA, "First known recording of the vocalizations of the Slender-billed Wren, *Hylorchilus sumichrasti,* and its bearing on the relationships of this species."

Albert E. Burchsted, Biology Dept., College of Staten Island, 715 Ocean Terr., Staten Island, NY, and Rosemary Gnam, Dept. Biology, Queens College, Queens, NY, "House Finch song institutions along the Hudson River valley."

Gary L. Ritchison, Dept. Biological Sciences, Eastern Kentucky Univ., Richmond, KY, "The singing behavior of female Northern Cardinals."

Lowell H. Suring, Jackie Canterbury, and Treshell O'Keefe-Black, USDA Forest Service, Tongass National Forest, Ketchikan, AK, "Breeding birds of riparian woodlands in southeast Alaska."

W. C. McComb, G. A. McPeek, G. E. Jacoby, and P. L. Groetsch, Dept. Forestry, Univ. Kentucky, Lexington, KY, "Associations between birds and Appalachian tree communities."

Jeff Keller, NYCWRU, Cornell Univ., Ithaca, NY, "Trends in avian species richness and density during even-aged succession following clearcutting."

Craig W. Benkman, Dept. Biological Sciences, SUNY, Albany, NY, "On the cost of specialization for crossbills."

J. W. Johnston and K. L. Bildstein, Winthrop College, Rock Hill, SC and Baruch Inst., Univ. South Carolina, Columbia, SC, "The need for freshwater in spite of a salt gland."

John M. Shipley, Jr., Waterfowl Consultants, 721 East Tuckey Ln., Phoenix, AZ, "Ingested lead shot in waterfowl harvested in Idaho during the 1983–1984 and 1984–1985 hunting seasons."

William L. Lynch, P.O. Box 22, Big Hill, KY, "Time budget of nestlings, feeding observations, and telemetry data of the Turkey Vulture."

Lisa C. Huff and Malcolm C. Coulter, Savannah River Ecol. Lab., Drawer E, Aiken, SC, "Availability of Wood Stork prey in wet and dry years and its effect on reproduction."

Peter C. Frederick, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, "Chronic tidally-induced nest failure in a colony of White Ibises."

T. D. Pitts, Biology Dept., Univ. Tennessee at Martin, Martin, TN, "Nesting success of Eastern Bluebirds adjacent to roads and away from roads."

Craig W. Benkman, Dept. Biological Sciences, SUNY, Albany, NY, "The timing of crossbill reproduction."

Nancy Flood, Zoology Dept., Univ. Toronto, Toronto, ONT, "The effects of brood parasitism and nest piracy on Scott's Orioles."

David F. Westneat, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, "Extra-pair fertilizations in the Indigo Bunting (*Passerina cyanea*)."

Peter M. Fetterolf, Dept. Pharmacology, Vanderbilt Univ., Nashville, TN and Roger I. C. Hansell, Dept. Zoology, Univ. Toronto, Toronto, ONT, "Spite in Ring-billed Gulls."

Marcy F. Lawton and Robert O. Lawton, Biological Sciences, Univ. Alabama Huntsville, Huntsville, AL, "Heterochrony and the evolution of avian sociality."

Ralph W. Dexter, Kent State Univ., Kent, OH, "Nesting success of former 'helpers at the nest' in a colony of Chimney Swifts (*Chaetura pelagica*)."

Ken Meyer, Dept. Biology, Univ. North Carolina, Chapel Hill, NC, "Dependent Sharp-shinned Hawks (*Accipiter striatus*) parasitized by unrelated conspecific young."

Thomas E. Moorman and Guy A. Baldassarre, Dept. Zoology-Entomology, Auburn Univ., AL, "Effect of second broods on productivity of Wood Ducks in east central Alabama."

Charles P. Nicholson, TVA, Norris, TN, Paul B. Hamel, Tenn. Dept. Conservation, 701 Broadway, Nashville, TN, and Robert M. Hatcher, Tenn. Wildl. Res. Agency, Box 40747, Nashville, TN, "The Tennessee Breeding Bird Atlas."

Charles R. Smith, Lab. Ornithology, Cornell Univ., Ithaca, NY, "The New York State Breeding Bird Atlas."

A. R. Buckelew, Jr. and E. E. Hutton, Dept. Biology, Bethany College, Bethany, WV, "Mountaintop buildings: hazards for migrating birds."

Robert J. Cooper, Kevin M. Dodge, and Robert C. Whitmore, Div. Forestry, West Virginia Univ., Morgantown, WV, "The effect of a Dimlin application on southern Appalachian forest birds."

George A. Hall, Dept. Chemistry, West Virginia Univ., Morgantown, WV, "Birds of the southern Appalachians—opening remarks."

Kerry N. Rabenold and Patricia Parker Rabenold, Dept. Biological Sciences, Purdue Univ., West Lafayette, IN, "Altitudinal migration in Carolina Juncos: is social dominance important?"

Robert S. Mulvilhill, Carnegie Museum of Natural History, Powdermill Nature Reserve, Star Rt. S, Rector, PA, "Variation in the extent of first prebasic molt of Dark-eyed Juncos (*Junco hyemalis*)."

Philip C. Shelton, Clinch Valley College, Wise, VA, "Status of the avifauna of spruce-fir forests on Mt. Rogers, Virginia."

David S. Lee, North Carolina State Museum, P. O. Box 27647, Raleigh, NC, "Latitudinal and altitudinal frontiers: summer bird fauna of Grandfather Mountain, North Carolina."

Fred J. Alsop, III and Thomas F. Laughlin, Biological Sciences Dept., P.O. Box 23,590A, East Tennessee State Univ., Johnson City, TN, "Census of a breeding bird population in a virgin spruce-fir forest on Mt. Guyot, Great Smoky Mountains National Park, before and after balsam wooly aphid infestation."

Kevin M. Dodge and Robert J. Cooper, Div. Forestry, West Virginia Univ., Morgantown, WV, "Predicting and examining the impact of a gypsy moth outbreak on southern Appalachian forest birds."

Judith W. McIntyre, Utica College, Utica, NY, "Hello, I'm a loon."

## ATTENDANCE

ALABAMA: *Auburn,* Guy Baldassarre, Mary Carrington, Cathy Johnson, Tim Jones, Michael Losito, Carolyn Marn, Thomas E. Moorman, David Rave, John D. Thompson; *Huntsville,* Marcy Lawton, Robert O. Lawton; *Opelika,* Ralph Mirarchi.

ALASKA: *Ketchikan,* Lowell H. Suring.

ARIZONA: *Phoenix,* John M. Shipley, Jr.

COLORADO: *Ft. Collins,* Clait E. Braun.

DISTRICT OF COLUMBIA: *Washington,* Martha Cooper.

FLORIDA: *Gainesville,* Mary H. Clench, Michael W. Collopy, Thomas C. Edwards, John William Hardy, Ken Meyer, Susan Priess, Ann Venables, Tom Webber, Petra Bohall Wood; *Miami,* Peter C. Frederick.

GEORGIA: *Athens,* Craig W. Benkman, Scott M. Pearson; *Decatur,* Georgann Schmalz; *Statesboro,* Bill Lovejoy.

HAWAII: *Honolulu,* Sheila Conant.

INDIANA: *Hanover,* Dan Webster, Juanita Webster; *Notre Dame,* Doris Jane Watt; *W. Lafayette,* Kerry Rabenold, Robert N. Wiedenmann.

KANSAS: *Manhattan,* John L. Zimmerman.

KENTUCKY: *Lexington,* Bill McComb; *Richmond,* Gary Ritchison.

MARYLAND: *Bethesda,* John A. Pond, Nancy Pond; *Laurel,* Danny Bystrak, Sam Droege.

MASSACHUSETTS: *Sherborn,* Richard T. Darby.

MICHIGAN: *Ann Arbor,* Louise S. Storer, Robert W. Storer; *Grass Lake,* Harold Ratcliff; *Jackson,* Robert A. Whiting; *Pleasant Lake,* Hubert (Hugh) Zernickow; *Ypsilanti,* Herbert H. Caswell, Jr., Mrs. Herbert H. Caswell, Jr.

MISSISSIPPI: *Mississippi State,* Bette Jackson, Jerome A. Jackson.

MISSOURI: *Cape Girardeau,* Andrea Ivanovich, Pam Price, David A. Schwepker, Richard Stiehl, Jonathan Tipler, Bill Whitmar, II.

NEW YORK: *Brooklyn Heights,* Florence G. Nixon; *Ithaca,* Jeffrey K. Keller, Charles R. Smith; *Lansing,* Helen Lapham; *Staten Island,* Albert E. Burchsted; *Utica,* Judith W. McIntyre.

NORTH CAROLINA: *Chapel Hill,* RoseMarie E. Etemad-Green, Michael T. Green, Helmut C. Mueller, Walter H. Piper, David F. Westneat; *Durham,* Nancy S. Mueller; *Raleigh,* Dave Lee.

OHIO: *Columbus,* Sandra L. Gaunt, Minna Hsu, John A. Smallwood, Thomas A. Waite, Jim Wood, Mark S. Woodrey; *Gambier,* Robert D. Burns; *Kent,* Ralph W. Dexter; *Lakewood,* Nancy R. Klamm, William A. Klamm; *Toledo,* John Kusnier, Jr., Elliot J. Tramer.

PENNSYLVANIA: *Chester Springs,* Berrell (Babs) Street, Phillips B. Street; *Hatfield,* Harry W. Mankonen; *Indiana,* Robert E. Merritt, Anthony J. Nastase; *Pittsburgh,* D. Scott Wood; *Rector,* Robert S. Mulvihill.

TENNESSEE: *Crossville,* Bruce Anderson; *Elizabethton,* Gary O. Wallace; *Franklin,* Stephen J. Stedman; *Johnson City,* Fred J. Alsop, III, Rick Knight; *Knoxville,* Laurie Armstrong, Mark Armstrong, Marcia Davis, Barbara Finney, Audrey R. Hoff, Ronald D. Hoff, Beth Lacy, J. B. Owen, James T. Tanner, Bill Yambert; *Lookout Mountain,* Jerome Wenger; *Martin,* David Pitts; *Maryville,* Ralph J. Zaenglein; *McKinsey,* Don Manning, Gina Manning; *Memphis,* Fred Carney, Ben B. Coffey, Jr., Lula C. Coffey. James A. Ferguson, George R. Payne, Jr., Wendall Whittemore; *Morristown,* Allen E. Ricks; *Nashville,* Sandra D. Bivens, Peter M. Fetterolf, Katherine A. Goodpasture, Paul Hamel, Robert Hatcher, Ann Tarbell, David F. Vogt; *Norris,* Linda J. Fowler, Charles P. Nicholson.

SOUTH CAROLINA: *Aiken,* Jeannine Angerman, Malcolm C. Coulter, Lisa C. Huff; *Chester,* Mrs. W. C. Stone, Sr.; *Rock Hill,* Keith L. Bildstein, Dale Gawlik, James W. Johnston; *Mt. Pleasant,* Robert Hooper; *Six Mile,* Douglas Branch McNair; *Spartanburg,* Miller C. Foster, Jr.

TEXAS: *Nacogdoches,* Richard N. Conner.

VIRGINIA: *Blacksburg,* Jerry W. Via; *Charlottesville,* Bill Akers; *Harrisonburg,* Kathleen H. Finnegan, Michael J. Finnegan; *Reston,* Henry Bell; *Williamsburg,* Ruth A. Beck, Lois E. Byrd, Mitchell A. Byrd.

WEST VIRGINIA: *Bethany,* Albert (Jay) Buckelew; *Elkins,* Eugene E. Hutton; *Morgantown,* Robert Cooper, Kevin Dodge, George A. Hall.

ONTARIO: *Toronto,* Jon C. Barlow, Nancy J. Flood, Thomas S. Parsons, Jim Rising, Vincent St. Louis.

SASKATCHEWAN: *Saskatoon,* William J. Maher.

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# ANNOUNCEMENTS

## SIGURD T. OLSON COMMON LOON RESEARCH AWARD

Wisconsin Project Loon Watch is accepting applications for its second annual award for research on Common Loons in the Lake Superior-Lake Michigan region of the United States and Canada. To apply for the $1000 award, a brief description (maximum 10 pp.) of the proposed research program and curriculum vitae should be submitted by the principal investigator to Dr. Paul I.V. Strong, Coordinator, Wisconsin Project Loon Watch, Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806 no later than 15 February 1987. Guidelines for prospective applicants can be requested from WPLW. Proposals by students should be accompanied by 2 letters of recommendation. The award will be granted on the basis of the project's potential to increase our understanding of the Upper Great Lakes populations of Common Loons.

## ROGER TORY PETERSON INSTITUTE CREATED

The Roger Tory Peterson Institute for the Study of Natural History began full-scale operations this year. The Institute's primary mission is to develop programs to increase the number of serious students of natural history. The Institute, in Jamestown, New York, near Lake Chautauqua, has been designated as the permanent repository for Roger Tory Peterson's artwork, correspondence, slides, movies, and other materials related to his remarkable lifetime achievements.

A $5-million headquarters facility is currently being designed, with a mid-1988 opening projected. The building will contain permanent and temporary exhibit areas for wildlife art shows (RTP's and other artists), dramatic displays on worldwide natural history, a 400-seat auditorium with 70 mm film-capability, an extensive natural history library, and research collections of natural history materials. The Institute's staff will eventually include 45 scientists, program coordinators, writers, and editors, with a mission of developing a high-quality, unique program of natural history experiences and publications on a worldwide scale.

Information about the Institute and its membership program may be obtained by writing: Roger Tory Peterson Institute, 525 Falconer Street, Jamestown, New York 14701. (716) 665-5220 ext. 448, or 665-3794.

## NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the fourth annual grants-in-aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants of single or multiple awards totaling $5000.00 are awarded and include:

*Bluebird Research Grant.*—Available to student, professional, or individual researchers

for a suitable research project focused on any of the three species of bluebird from the genus *Sialia.*

*General Research Grant.*—Available to student, professional, or individual researchers for a suitable research project focused on a North American cavity-nesting species.

*Student Research Grant.*—Available to full-time college or university students for a suitable research project focused on a North American cavity-nesting species.

Further guidelines and application materials are available upon request from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746.

The North American Bluebird Society is proud to announce the presentation of the third annual research grant awards. The 1986 recipients are as follows:

*BLUEBIRD GRANTS.*—Anthony J. Savereno (Topic: Movements and Habitat Use of Juvenile Eastern Bluebirds) and R. Craig Hensley (Topic: Predation of Eastern Bluebird Nests by Black Rat Snakes Based on Nestbox Location)

*GENERAL GRANTS.*—Jeffrey R. Waters (Topic: A Comparative and Experimental Study of the Nesting Habitat of a Cavity-Nesting Bird Community) and Gregg Zuberbier (Topic: Effects of Blowfly *Protocalliphora* sp. Larvae on Nestling Passerines in both Laboratory and Natural Environments)

Barry A. Bermudez (Topic: Development of a House Sparrow—Starling proof Nest Box Design that is Acceptable to Native Cavity Nesters)

*STUDENT GRANT.*—Karen J. Wilson (Topic: Validating a Pileated Woodpecker Habitat Suitability Index Model for the Northern Rocky Mountains)

## A NEW JOURNAL COVERING AFRICAN RAPTORS

GABAR (Growth and Biology of African Raptors) is a new journal publishing material on African raptors, here defined as eagles, hawks, harriers, buzzards, falcons, and owls (i.e., excluding vultures, seabirds, and other predatory birds already covered by specialist publications in the region). Contents will include short papers on completed studies, progress reports on ongoing research, short notes, unusual sightings, conservation problems, and a Forum in which opinions, continuing controversies, constructive criticism, and new ideas are aired and challenged. The first edition has been printed and copies can be obtained free of charge from the address below. Subsequent editions will be distributed on receipt of a subscription fee. Write Robert Simmons, Editor—GABAR, Dept. Zoology, Univ. Witwatersrand, Johannesburg 2001, Republic of South Africa.

# INDEX TO VOLUME 98, 1986

By Kathy G. Beal

This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Common names are as they appear in the volume unless otherwise specified. Reference is made to books reviewed and announcements as they appear in the volume.


Accipiter cooperii, 110–115, 116–125
  gentilis, 110–125
  nisus, 110, 117
  striatus, 110, 119–125, 211, 568
Actitis macularia, 35, 474
Aegolius acadicus, 387–406
  funereus, 387–406, 558
Agelaius phoeniceus, 115, 231–242, 257–266, 604
  xanthomus, 126–131
age
  of mated pairs of Larus californicus, 610–612
age-specific foraging ability in Larus philadelphia, L. delawarensis, and L. argentatus, 267–279
Aguilar, Pedro G., F., see Stiles, F. Gary and ———
Ailuroedus buccoides, 511
Aix sponsa, 167–168
Albatross, Waved, see Diomedea irrorata
albinism
  in Puffinus gravis, 488–490
Alca torda (Frontispiece, opposite 189)
Allen, George T., Robert K. Murphy, Karen Steenhof, and Stephen W. Platt, Late fledging dates, renesting, and large clutches of Prairie Falcons, 463–465
Amazilia amabilis, 38–60
  edward, 38–60
  tzacatl, 38–60
  violiceps, 353–367
Amazona autumnalis, 38–60
  vittata, 126
Ammodramus aurifrons, 596
  humeralis, 596
  maritimus, 380
  savannarum, 596
  spp., 596
Amphispiza belli, 535–546
Anas americana, 306, 438
  crecca, 438
  platyrhynchos, 608–609
  strepera, 306
  superciliosa, 307
Andrewartha, H. G. and L. C. Birch, The ecological web, reviewed, 495–497
Anhima cornuta, 243–256
announcements
  Call for assistance, 504
  New journal covering African raptors, 640
  Roger Tory Peterson Institute created, 639
  Second international symposium on breeding birds in captivity, 504
  Second Vice-Presidents of the Wilson Ornithological Society, 333
  Third World Conference on Birds of Prey, 504
Anous stolidus, 588–591
Anseranas semipalmata, 249, 255
Antbird, Bicolored, see Gymnopithys leucaspis
  Chestnut-backed, see Myrmeciza exsul
  Dusky, see Cercomacra tyrannina
  Ocellated, see Phaenostictus mcleannani
  Spotted, see Hylophylax naevioides
  White-bellied, see Myrmeciza longipes
Antshrike, Fasciated, see Cymbilaimus lineatus
  Slaty, see Thamnophilus punctatus
Ant-tanager, Red-throated, see Habia fuscicauda
Antthrush, Black-faced, see Formicarius analis
Antwren, Ash-throated, see Herpsilochmus parkeri
  Black-capped, see Herpsilochmus atricapillus
  Checker-throated, see Myrmotherula fulviventris

Dot-winged, see Microrhopias quixensis
White-browed, see Herpsilochmus pileatus
White-flanked, see Myrmotherula axillaris
Yellow-bellied, see Herpsilochmus motacilloides
Apel, Karen M. and Charles M. Weise, The hiss-display of nestling Black-capped Chickadees in captivity, 320–321
Aphelocoma ultramarina, 364
Aquila chrysaetos, 117, 136, 445–458, 600–601
Aracari, Collared, see Pteroglossus torquatus
Archilochus alexandri, 353–367
colubris, 163–167
Arenaria interpres, 101–109
Arremonops conirostris, 38–60
Asio flammeus, 117–125, 387–406
otus, 387–406, 547–560
Athene cunicularia, 387–406
noctua, 387–406
Atlapetes spp., 596
Attila, Bright-rumped, see Attila spadiceus
Attila spadiceus, 38–60
Aulacorhynchus prasinus, 585–588
Automolus ochrolaemus, 38–60, 343
avifauna
of Yucatán, Mexico, 163–167
Avocet, American, see Recurvirostra americana
awards and grants
First George Miksch Sutton award for ornithological art, 333
Hawk Mountain research award, 504
North American Bluebird Society research grants, 639–640
North American Loon Fund grants, 418
Sigurd T. Olson Common Loon research award, 639
Student membership awards, 334
Aythya affinis, 433–444
americana, 306
australis, 307
collaris, 306–307
ferina, 434
marila, 433–444
valisineria, 306–307, 434
Babbler, Rufous, see Pomatostomus isidorei
Baird, Pat, A new method for collecting prey delivered to Tufted Puffin chicks, 169–170
Baker, R. Robin, Bird navigation: the solution of a mystery?, reviewed, 177–178
Baltosser, William H., Nesting success and productivity of hummingbirds in southwestern New Mexico and southeastern Arizona, 353–367
Banks, Richard C., Subspecies of the Greater Scaup and their names, 433–444
Barlow, Jon C., see Bortolotti, Gary R. and ———
Barn-Owl, Common, see Tyto alba
Bartramia longicauda, 474
Baryphthengus ruficapillus, 38–60
Beehler, Bruce M. and Carol H. Beehler, Observations on the ecology and behavior of the Pale-billed sicklebill, 505–515
Beehler, Bruce M., see Ripley, S. Dillon and ———
Beehler, Carol H., see Beehler, Bruce M. and ———
behavior
aggression
between female Pheucticus melanocephalus, 486–488
bathing
by Chordeiles minor, 612–613
copulatory
reverse mounting in Falco sparverius, 472–473
courtship
of Phalacrocorax albiventer and P. atriceps, 571–580
dispersal
of recently fledged Zenaida macroura, 581–585
display
hiss-display of nestling Parus atricapillus, 320–321
of male Epimachus bruijnii, 513
distraction
of Charadrius vociferus, 605–607
drinking
by Colinus virginianus, 485–486
feeding
distributing food to Hirundo rustica broods, 286–291
food-related

Circus cyaneus takes Lagopus lagopus albus, 597–600
collecting prey delivered to Fratercula cirrhata, 169–170
Dendragapus obscurus eats Gerrhonotus coeruleus, 171–172
Picoides pubescens takes insects from spider web, 319
robbery of Aythya collaris by Fulica americana, 306–308
foraging, see foraging behavior
incubation
in Zenaida macroura, 297–300
leading
of Anas platyrhynchos pairs, 608–609
nesting
trios of Zenaida macroura, 309–311
reproductive
assortative mating in Sterna hirundo, 93–100
brood adoption by male Parus atricapillus, 312–313
brood mixing by Gavia immer, 478–479
of Accipiter cooperii, 110–115
of Dendroica petechia, 152–154
of Falco mexicanus, 463–465
of Tachycineta bicolor, 147–150, 150–152
two male Dolichonyx oryzivorus feed young at same nest, 154–156
territorial
of Pooecetes gramineus, 144–147
Bekoff, Marc, see Fee, Barbara A. and ———
Bell, Patricia A., see Merritt, Robert E., ———, and Victorin Laboudallon
Belles-Isles, Jean-Claude and Jaroslav Picman, Destruction of heterospecific eggs by the Gray Catbird, 603–605
Bentbill, Southern, see Oncostoma olivaceum
Bergan, James F. and Loren M. Smith, Food robbery of wintering Ring-necked Ducks by American Coots, 306–308
Best, Louis B., see Petersen, Kenneth L., ———, and Brian M. Winter
Best, Louis B., see Stauffer, Dean F. and ———
Best, Louis B., see Westmoreland, David and ———
Bildstein, Keith L., reviews by, 186–187, 495–496, 502
Birch, L. C., see Andrewartha, H. G. and ———
Bird of Paradise, King, see Cicinnurus regius
Lesser, see Paradisaea minor
Superb, see Lophorina superba
Twelve-wired, see Selucidis melanoleuca
Birkhead, T. R., see C. M. Perrins and ———
Bissonette, John A., see Strong, Paul I. V., ———, and Richard Souza
Blackbird, Brewer's, see Euphagus cyanocephalus
Red-winged, see Agelaius phoeniceus
Yellow-shouldered, see Agelaius xanthomus
Blake, John G., Species-area relationship of migrants in isolated woodlots in east-central Illinois, 291–296
Blockstein, David E., Nesting trios of Mourning Doves, 309–311
Bluebird, Eastern, see Sialia sialis
Western, see Sialia mexicana
bobcat, see Felix rufus
Bobolink, see Dolichonyx oryzivorus
Bobwhite, Northern, see Colinus virginianus, 485–486
Boehme, R. L., see Flint, V. E., ———, Y. V. Kostin, and A. A. Kuznetzov
Bollinger, Eric K., Thomas A. Gavin, Catherine J. Hibbard, and J. Timothy Wootton, Two male Bobolinks feed young at the same nest, 154–156
Bombycilla cedrorum, 115, 615
Bonasa umbellus, 61–82, 89, 425, 427
Booby, Blue-footed, see Sula nebouxii
Masked, see Sula dactylatra
Bortolotti, Gary R. and Jon C. Barlow, Potential use of feather chemistry as an indicator of relative growth, 516–525
Bos taurus, 158
Bowman, Reed and Elizabeth M. Curley, Reverse mounting in the American Kestrel, 472–473
Branta canadensis, 523
Braun, Clait E., review by, 492–493

Braun, Clait E., see Dunn, Peter O. and ———
breeding biology
of Agelaius phoeniceus, 257–266
of Aulacorhynchus prasinus, 585–588
of Coracopsis nigra barklyi, 160–163
of polygamous Charadrius alexandrinus, 15–37
sperm release in northern thrushes, 526–534
Brooke, R. K., South African red data book—birds, reviewed, 181–182
Brotogeris jugularis, 38–60
Brunton, Dianne H., Fatal antipredator behavior of a Killdeer, 605–607
Bruun, Bertel, Common birds of Egypt, reviewed, 500
Bubo bubo, 387–406
virginianus, 69, 101–109, 121, 124, 387–406, 467, 553
Bubulcus ibis, 300
Bucco macrorhynchos, 38–60
Bucephala albeola, 438
clangula, 167–168
Buckelew, Albert R. J., review by, 624
Buckley, F. G., see Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgley, and ———
Buckley, P. A., M. S. Foster, E. S. Morton, R. S. Ridgley, and F. G. Buckley, eds., Neotropical ornithology, reviewed, 616–625
Budgerigar, see Melopsittacus undulatus
Bufflehead, see Bucephala albeola
Bull, John, Birds of New York state, reviewed, 498
Bunting, Indigo, see Passerina cyanea
Painted, see Passerina ciris
Burton, Robert, Bird behavior, reviewed, 493–494
Buteo jamaicensis, 65, 69, 116–125, 561–570
lagopus, 118
lineatus, 119–125, 466–469
platypterus, 38–60, 119–125, 469–471, 568
regalis, 117
swainsoni, 119–125
Butler, P. J., see Phillips, J. G., ———, and P. J. Sharp
Butorides striatus, 613–614
Cacicus uropygialis, 38–60
Cacique, Scarlet-rumped, see Cacicus uropygialis
Cairns, D. K., see Gaston, A. J., ———, R. D. Elliot, and D. G. Noble
Calder, William A., III, review by, 619–621
Calidris alpina, 35
temminckii, 35
Callipepla californica, 110, 111
Calonectris diomedea, 488
Calypte anna, 613
costae, 353–367
Campbell, Bruce and Elizabeth Lack, eds., A dictionary of birds, reviewed, 322–323
Campbell, Louis W., see Tramer, Elliot J. and ———
Campbell, R. W., E. D. Forsman, and B. M. Van Der Raay, An annotated bibliography of literature on the Spotted Owl, reviewed 331
Canis familiaris, 600
latrans, 136
Canvasback, see Aythya valisineria
Capercaillie, see Tetrao urogallus
Cardinal, Northern, see Cardinalis cardinalis
Cardinalis cardinalis, 231–242
Carduelis pinus, 214–230
spp., 321
Carpodacus mexicanus, 459–462
purpureus, 214–230
sp., 115
Casmerodius albus, 476
Catbird, Gray, see Dumetella carolinensis
White-eared, see Ailuroedus buccoides
Cathartes aura, 118, 157–160, 600–601
Catharus fuscescens, 526–534
guttatus, 214–230
minimus, 526–534, 615
ustulatus, 38–60, 163–167, 320, 526–534
Catoptrophorus semipalmatus, 473–475
Centrocercus urophasianus, 83–92, 426–427, 429
Cercomacra tyrannina, 38–60
Certhia americana, 214–230
Chachalaca, Gray-headed, see Ortalis cinereiceps
Chalybura buffonii, 38–60
Charadrius alexandrinus, 15–37
melodus, 23, 474

montanus, 35
vociferus, 23, 474, 605–607
wilsonia, 29
Charitospiza spp., 594–597
Chauna chavaria, 243
torquata, 252–255
Chen caerulescens, 93
Chickadee, Black-capped, see Parus atricapillus
Chestnut-backed, see Parus rufescens
Mountain, see Parus gambeli
chicken, domestic, see Gallus gallus, Gallus domesticus, and Gallus sp.
chipmunk, see Tamias striatus
Townsend's, see Tamias townsendi
Chloroceryle aenea, 38–60
Chlorophanes spiza, 38–60
Chordeiles minor, 612–613
Cicinnurus regius, 510
Circus cyaneus, 116–125, 597–600
Cistothorus palustris, 604
platensis, 604
Clapp, Roger B., Great-tailed Grackle kills Barn Swallow in flight, 614–615
Claravis pretiosa, 38–60
Clark, George A., Jr., Systematic interpretations of foot-scute patterns in Neotropical finches, 594–597
clutch size
of Carpodacus mexicanus, 459–462
of Falco mexicanus, 463–465
Cnemoscopus rubrirostris, 594
Cnipodectes subbrunneus, 38–60
Coccothraustes vespertinus, 214–230, 308
Coccyzus americanus, 163–167
erythropthalmus, 163–167
Cody, Ronald P. and Jeffrey K. Smith, Applied statistics and the SAS programming language, reviewed, 186–187
Cohen, Robert R. and Mark L. Dymerski, Swallows taking insects from pond surfaces, 483–484
Colaptes auratus, 115, 214–230
Coleman, John S. and James D. Fraser, Predation on Black and Turkey vultures, 600–601
Colinus virginianus, 485–486
Collopy, Michael W., Food consumption and growth energetics of nestling Golden Eagles, 445–458
color
variation in Oxyura jamaicensis andina, 592–594
Columba fasciata, 115
leucocephala, 582
livia, 168–169
palumbus, 582
speciosa, 38–60
Colwell, Mark A., Intraspecific brood parasitism in three species of prairie-breeding shorebirds, 473–475
community structure
in even-aged forest stands, 61–82
in forest during summer and winter, 214–230
Contopus borealis, 115, 214–230
sordidulus, 214–230
virens, 163–167, 231–242
Coot, American, see Fulica americana
Eurasian, see Fulica atra
Coracopsis nigra barklyi, 160–163
Coragyps atratus, 157–160, 600–601
Cormorant, Flightless, see Nannopterum harrisi
Olivaceous, see Phalacrocorax olivaceus
Corvus brachyrhynchos, 25, 292, 298, 299
caurinus, 115
corax, 463
Cotinga, Blue, see Cotinga nattererii
Cotinga nattererii, 38–60
cottontail, eastern, see Sylvilagus floridanus
Coturnix chinensis, 604
coturnix, 604
Coulter, Malcolm C., Assortative mating and sexual dimorphism in the Common Tern, 93–100
cow, see Bos taurus
Cowbird, Brown-headed, see Molothrus ater
Shiny, see Molothrus bonariensis
coyote, see Canis latrans
Crane, Sandhill, see Grus canadensis
Creagrus furcatus, 588–591
Creeper, Brown, see Certhia americana
Crow, American, see Corvus brachyrhynchos
Northwestern, see Corvus caurinus
Crypturellus soui, 38–60
Cuckoo, Black-billed, see Coccyzus erythropthalmus
Pheasant, see Dromococcyx phasianellus

Squirrel, see Piaya cayana
Yellow-billed, see Coccyzus americanus
Curley, Elizabeth M., see Bowman, Reed and ———
Cyanerpes cyaneus, 38–60
Cyanocitta cristata, 61–82, 210, 231–242, 407–418
stelleri, 214–230
Cyanocompsa cyanoides, 38–60
Cymbilaimus lineatus, 38–60
Cynanthus latirostris, 353–367
Cyphorhinus phaeocephalus, 38–60
Dacnis, Blue, see Dacnis cayana
Scarlet-thighed, see Dacnis venusta
Dacnis cayana, 38–60
venusta, 38–60
Damophila julie, 38–60
Davis, Tristan J. and John P. O'Neill, A new species of antwren (Formicariidae: Herpsilochmus) from Peru, with comments on the systematics of other members of the genus, 337–352
Davis, William E., Jr., Effects of old nests on nest-site selection in Black-crowned Night-Herons and Snowy Egrets, 300–303
deer, white-tailed, see Odocoileus virginianus
Delichon urbica, 389, 483, 542
DellaSala, Dominick A., Polygyny in the Yellow Warbler, 152–154
Dendragapus canadensis, 83, 427, 429
obscurus, 83, 171–172, 419–432
Dendrocincla fuliginosa, 38–60
homochroa, 38–60
Dendroica caerulescens, 196–213
castanea, 38–60
coronata, 163–167, 210, 214–230, 488
discolor, 154
dominica, 163–167
fusca, 196–213
magnolia, 38–60, 163–167
occidentalis, 214–230
palmarum, 163–167
pensylvanica, 38–60, 61–82, 163–167
petechia, 126–131, 152–154, 163–167, 315–317, 321, 604
virens, 163–167, 196–213
Dennis, John V., The wildlife gardener, reviewed, 624
density
of seabirds during the 1983 El Niño, 588–591
Derrickson, Kim C., Which sex leads in paired Mallards?, 608–609
Diamond, A. W. and T. E. Lovejoy, eds., Conservation of tropical forest birds, reviewed, 491–492
Dickcissel, see Spiza americana
Dickerman, Robert W., review by, 327–328
Dicrurus hottentottus, 510
Didelphis virginiana, 158, 600
Diem, Kenneth L., see Pugesek, Bruce and ———
diet
Cathartes aura, 157–160
Coragyps atratus, 157–160
Passer domesticus, 137–144
wax digestion by Oceanites oceanicus, 189–195
Dinsmore, James J., see Johnson, Rex R. and ———
Diomedea irrorata, 588–591
Diuca spp., 595
Dodge, Kevin M., review by, 500–501
dog, see Canis familiaris
Dolichonyx oryzivorus, 154–156
Dolospingus spp., 594–597
Dove, Gray-chested, see Leptotila cassini
Mourning, see Zenaida macroura
Rock, see Columba livia
White-tipped, see Leptotila verreauxi
White-winged, see Zenaida asiatica
Drepanornis spp., 514
Drewry, C. Gerald, see Vogt, David F., ———, Paul B. Hamel, and Stephen J. Stedman
Dromococcyx phasianellus, 38–60
Drongo, Spangled, see Dicrurus hottentottus
Dryocopus lineatus, 38–60
pileatus, 214–230
Duck, Mallard, see Anas platyrhynchos
Pacific Black, see Anas superciliosa
Ring-necked, see Aythya collaris
Ruddy, see Oxyura jamaicensis andina
Wood, see Aix sponsa
Ducula spilorrhoa, 299
Duffy, David Cameron and Godfrey Merlen, Seabird densities and aggregations during the 1983 El Niño in the Galapagos Islands, 588–591
Duffy, David Cameron, Rory P. Wilson,

Marie-Pierre Wilson, and Claudio Velasquez R., Plunge-diving by Olivaceous Cormorants in Chile, 607–608
Dumetella carolinensis, 38–60, 61–82, 163–167, 231–242, 603–605
Dunlin, see Calidris alpina
Dunn, Erica, review by, 174–175
Dunn, Peter O. and Clait E. Braun, Late summer-spring movements of juvenile Sage Grouse, 83–92
Dymerski, Mark L., see Cohen, Robert R. and ———
Eagle, Bald, see Haliaeetus leucocephalus
Golden, see Aquila chrysaetos
Eagle-Owl, European, see Bubo bubo
egg
cryptic coloration
in Zenaida macroura, 297–300
destruction
by Dumetella carolinensis, 603–605
by Eudocimus albus, 156–157, 476–478
loss
in Sterna hirundo, 101–109
Egret, Cattle, see Bubulcus ibis
Great, see Casmerodius albus
Snowy, see Egretta thula
Egretta caerulea, 300, 482–483, 557
thula, 300–303
tricolor, 300
Elaphe obsoleta obsoleta, 602–603
Elliot, R. D., see Gaston, A. J., D. K. Cairns, ———, and D. G. Noble
Empidonax flaviventris, 163–167
hammondii, 214–230
minimus, 163–167, 196–213
oberholseri, 214–230, 311–312
sp., 115
traillii, 38–60, 311–312
virescens, 38–60, 163–167
Epimachus albertisi, 507, 513–514
bruijnii, 505–515 (Frontispiece)
fastuosus, 514
meyeri, 513–514
erratum, 92
Eucometis penicillata, 38–60
Eudocimus albus, 156–157, 284, 476–478
Eugenes fulgens, 353–367
Euphagus cyanocephalus, 115
Euphonia fulvicrissa, 38–60
Euphonia, Fulvous-vented, see Euphonia fulvicrissa
Euxenura maguari, 476
Evans, P. R., J. D. Goss-Custard, and W. G. Hale, eds., Coastal waders and wildfowl in winter, reviewed, 175–176
Falco columbarius, 117–125
mexicanus, 122, 463–465
novaeseelandiae, 119
peregrinus, 117–125, 464
sparverius, 116–125, 454, 472–473
Falcon, New Zealand, see Falco novaeseelandiae
Peregrine, see Falco peregrinus
Prairie, see Falco mexicanus
Fantail, Rufous-backed, see Rhipidura rufidorsa
Fee, Barbara A. and Marc Bekoff, Polygyny in the Evening Grosbeak, 308
Felis rufus, 553
Ficken, Millicent S., review by, 493–494
Finch, Darwin's, see Geospiza fortis
House, see Carpodacus mexicanus
Medium Ground, see Geospiza fortis
Fitzpatrick, John W. and John P. O'Neill, Otus petersoni, a new Screech-Owl from the Eastern Andes, with systematic notes on O. colombianus and O. ingens, 1–14
Fitzpatrick, John W., see Woolfenden, Glen E. and ———
Fjeldså, Jon, Color variation in the Ruddy Duck (Oxyura jamaicensis andina), 592–594
Flatbill, Olivaceous, see Rhynchocyclus olivaceus
Flicker, Common, see Colaptes auratus
Flint, V. E., R. L. Boehme, Y. V. Kostin, and A. A. Kuznetzov, A field guide to birds of the USSR, reviewed, 178–179
Florisuga mellivora, 38–60
Flycatcher, Acadian, see Empidonax virescens
Black-tailed, see Myiobius atricaudus
Boat-billed, see Megarhynchus pitangua
Brownish, see Cnipodectes subbrunneus
Dusky, see Empidonax oberholseri
Dusky-capped, see Myiarchus tuberculifer
Great Crested, see Myiarchus crinitus
Hammond's, see Empidonax hammondii

Least, see Empidonax minimus
Northern Royal, see Onychorhynchus mexicanus
Ochre-bellied, see Mionectes oleagineus
Olive, see Microeca flavovirescens
Olive-sided, see Contopus borealis
Panama, see Myiarchus panamensis
Ruddy-tailed, see Terenotriccus erythrurus
Social, see Myiozetetes similis
Streaked, see Myiodynastes maculatus
Willow, see Empidonax traillii
Yellow-bellied, see Empidonax flaviventris
Foliage-gleaner, Buff-throated, see Automolus ochrolaemus
food consumption
of nestling Aquila chrysaetos, 445–458
foraging behavior
age-specific ability in Larus philadelphia, L. delawarensis, and L. argentatus, 267–279
Butorides striatus baits fish with insects, 613–614
of Epimachus bruijnii, 507
of nesting male and female Accipiter cooperii, 110–115
plunge-diving by Phalacrocorax olivaceus, 607–608
sex differences in forest birds, 196–213
success of Missouri raptors, 116–125
swallows taking insects from pond surfaces, 483–484
Forest-Falcon, Collared, see Micrastur semitorquatus
Formicarius analis, 38–60
Forsman, E. D., see Campbell, R. W., ———, and B. M. Van Der Raay
Foster, M. S., see Buckley, P. A., ———, E. S. Morton, R. S. Ridgley, and F. G. Buckley
fox, red, see Vulpes vulpes
Fratercula cirrhata, 169–170
Fraser, James D., see Coleman, John S. and ———
Frederick, Peter, Conspecific nest takeovers and egg destruction by White Ibises, 156–157
Frederick, Peter C. and Mark A. Shields, Suspected intraspecific egg dumping in the White Ibis (Eudocimus albus), 476–478
Fregata magnificens, 588
minor, 588
spp., 588–591
Frigatebird, Great, see Fregata minor
Magnificant, see Fregata magnificens
Friedman, Herbert and Lloyd F. Kiff, The parasitic cowbirds and their hosts, reviewed, 328
frogmouth, see Podargus sp.
Frohring, Paula C., see Kushlan, James A. and ———
Fruitcrow, Purple-throated, see Querula purpurata
Fulica americana, 306–308
atra, 307
Fuligula mariloides, 433–444
Gadwall, see Anas strepera
Gallinago gallinago, 474
Gallus domesticus, 604
gallus, 158
sp., 115
gannet, see Morus spp.
Garcia, Jesús, B., see Rogers, David T., Jr., ———, and Antonio Rógel B.
Garrison, Barrett A., Catherine Vouchilas, and Dean F. Stauffer, Nestling Great Crested Flycatcher parasitized by larval fly (Protocalliphora hirudo), 321
Gaston, A. J., D. K. Cairns, R. D. Elliot, and D. G. Noble, A natural history of the Digges Sound, reviewed, 331
Gavett, Ann P. and James S. Wakeley, Diets of House Sparrows in urban and rural habitats, 137–144
Gavia immer, 478–479
Gavin, Thomas A., see Bollinger, Eric K., ———, Catherine J. Hibbard, and J. Timothy Wootton
Geospiza fortis, 93, 541
Geothlypis trichas, 61–82, 163–167, 231–242
Gerrhonotus coeruleus, 171–172
Glaucidium brasilianum, 387–406
gnoma, 387–406
passerinum, 387–406
Glaucis hirsuta, 38–60
Glyphorhynchus spirurus, 38–60
Gnatcatcher, Tropical, see Polioptila plumbea

Gnatwren, Long-billed, see Ramphocaenus melanurus
Godwit, Marbled, see Limosa fedoa
Goldeneye, Common, see Bucephala clangula
Goldfinches, see Carduelis spp.
Gooders, John, Birds that came back, reviewed, 500–501
Goose, Canada, see Branta canadensis
Magpie, see Anseranas semipalmata
Snow, see Chen caerulescens
Goss-Custard, J. D., see Evans, P. R., ———, and W. G. Hale
Graber, Jean, W., Richard R. Graber, and Ethelyn L. Kirk, Illinois birds: vireos, reviewed, 332
Graber, Richard R., see Graber, Jean W., ———, and Ethelyn L. Kirk
Grackle, Boat-tailed, see Quiscalus major
Common, see Quiscalus quiscula
Greater Antillean, see Quiscalus niger
Great-tailed, see Quiscalus mexicanus
Grant, Gilbert S., see Lee, David S. and ———
grants, see awards and ———
Grassquit, Blue-black, see Volatinia jacarina
Grosbeak, Black-headed, see Pheucticus melanocephalus
Blue, see Guiraca caerulea
Blue-black, see Cyanocompsa cyanoides
Evening, see Coccothraustes vespertinus
Rose-breasted, see Pheucticus ludovicianus
Ground-Dove, Blue, see Claravis pretiosa
Grouse, Black, see Lyrurus tetrix
Blue, see Dendragapus obscurus
Red, see Lagopus lagopus scoticus
Ruffed, see Bonasa umbellus
Sage, see Centrocercus urophasianus
Sharp-tailed, see Tympanuchus phasianellus
Spruce, see Dendragapus canadensis
growth
energetics of nestling Aquila chrysaetos, 445–458
of nestling Molothrus bonariensis and host nestlings, 126–131
of nestling Amphispiza belli and Spizella breweri, 535–546
use of feather chemistry as an indicator of, 516–525
Grus canadensis, 131–137
Guiraca caerulea, 163–167
Gull, Bonaparte's, see Larus philadelphia
California, see Larus californicus
Herring, see Larus argentatus
Laughing, see Larus atricilla
Lesser Black-backed, see Larus fuscus
Ring-billed, see Larus delawarensis
Swallow-tailed, see Creagrus furcatus
Guthery, Fred S., See Prasad, N. L. N. S. and ———
Gymnopithys leucaspis, 38–60
Habia fuscicauda, 38–60
habitat
structure
effect on territory of Pooecetes gramineus, 144–147
use
by Grus canadensis, 131–137
habitat selection
by Epimachus bruijnii, 505–507
Hailman, Jack P., review by, 176–177
Hale, W. G., see Evans, P. R., J. D. Goss-Custard, and ———
Haliaeetus leucocephalus, 119, 122, 456, 516–525, 600
Hall, George A., reviews by, 187–188, 188, 322–323, 328, 331, 332, 498, 501–502, 502–503, 503
Hamel, Paul B., see Vogt, David F., C. Gerald Drewry, ———, and Stephen J. Stedman
Hannon, Susan J., see Hik, David S., ———, and Kathy Martin
Haplospiza spp., 595
Hardhead, see Aythya australis
Hardy, John William, ed., Voices of the New World jays, crows, and their allies, family Corvidae, reviewed, 185–186
Hardy, John William, review by, 624–625
Hardy, John William and Theodore A. Parker III, Voices of the New World thrushes, reviewed, 502–503
Harrier, Northern, see Circus cyaneus
Harris, M. P., The Puffin, reviewed, 326
Hartford, Ronald, see Lumsden, Harry G., Judy Robinson, and ———
Hawk, Broad-winged, see Buteo platypterus

Cooper's, see Accipiter cooperii
Ferruginous, see Buteo regalis
Harris', see Parabuteo unicinctus
Red-shouldered, see Buteo lineatus
Red-tailed, see Buteo jamaicensis
Rough-legged, see Buteo lagopus
Sharp-shinned, see Accipiter striatus
Swainson's, see Buteo swainsoni
Hawk-Owl, Northern, see Surnia ulula
Hecht, M. K., J. H. Ostron, G. Viohl, and P. Wellnhofer, eds., The beginnings of birds. Proceedings of the International Archaeopteryx Conference Eichstätt 1984, reviewed, 618–619
Heliangelus regalis, 1
Hemitriccus cinnamomeipectus, 1
rufigularis, 343
Henicorhina leucoptera, 1
leucosticta, 38–60
Henry, J. David, see Scotter, George W., Wayne P. Neil, and ———
Hensley, R. Craig and Kimberly G. Smith, Eastern Bluebird responses to nocturnal black rat snake nest predation, 602–603
Hermit, Little, see Phaethornis longuemareus
Long-tailed, see Phaethornis superciliosus
Rufous-breasted, see Glaucis hirsuta
Heron, Green-backed, see Butorides striatus
Little Blue, see Egretta caerulea
Tricolored, see Egretta tricolor
Herpsilochmus atricapillus, 337–352 (Frontispiece)
axillaris, 337–352
dorsimaculatus, 337–352
longirostris, 337–352
motacilloides, 337–352 (Frontispiece)
parkeri, 337–352 (Frontispiece)
pectoralis, 337–352
pileatus, 337–352 (Frontispiece)
roraimae, 337–352
rufimarginatus, 337–352
stictocephalus, 344, 350
sticturus, 337–352
Hibbard, Catherine J., see Bollinger, Eric K., Thomas A. Gavin, ———, and J. Timothy Wootton
Hik, David S., Susan J. Hannon, and Kathy Martin, Northern Harrier predation on Willow Ptarmigan, 597–600
Hill, Geoffrey E., Severe aggression between female Black-headed Grosbeaks, 486–488
Hillstar, Andean, see Oreotrochilus estella
Hines, James E., Social organization, movements, and home ranges of Blue Grouse in fall and winter, 419–432
Hirundo pyrrhonota, 151, 286, 484
rustica, 151, 286–291, 483–484, 614–615
Hitchcock, Ronald R. and Ralph E. Mirarchi, Dispersal of recently fledged Mourning Doves from nest sites, 581–585
Holldobler, Bert and Martin Lindauer, eds., Experimental behavioral ecology and sociobiology, reviewed, 176–177
Hollett, Alan, review by, 500
Holmes, Richard T., Foraging patterns of forest birds: male-female differences, 196–213
home range
of Dendragapus obscurus, 419–432
of Epimachus bruijnii, 508–509
Honeycreeper, Green, see Chlorophanes spiza
Red-legged, see Cyanerpes cyaneus
Hoppe, Richard T. and Robert A. Kennamer, Little Blue Heron nesting among cattails, 482–483
Hosking, Eric, Wildfowl, reviewed, 621–622
House-Martin, Common, see Delichon urbica
Howitz, James L., Brood adoption by a male Black-capped Chickadee, 312–313
Hummingbird, Anna's, see Calypte anna
Black-chinned, see Archilochus alexandri
Blue-chested, see Amazilia amabilis
Broad-billed, see Cynanthus latirostris
Broad-tailed, see Selasphorus platycercus
Costa's, see Calypte costae
Magnificent, see Eugenes fulgens
Ruby-throated, see Archilochus colubris
Rufous-tailed, see Amazilia tzacatl
Snowy-bellied, see Amazilia edward
Violet-bellied, see Damophila julie
Violet-crowned, see Amazilia violiceps
Hutchinson, John N., Australian bird calls, reviewed, 624–625

Hylocichla mustelina, 38–60, 526–534
Hylophylax naevioides, 38–60
Ibis, White, see Eudocimus albus
Icterus chrysater, 38–60
  cucullatus, 364
  galbula, 38–60, 231–242
  spurius, 163–167
information for authors, 335–336
Ixoreus naevius, 214–230
Jacana, Northern, see Jacana spinosa
Jacana spinosa, 35
Jackson, Christine E., Bird etchings; the illustrators and their books, 1655–1855, reviewed, 622–623
Jacobin, White-necked, see Florisuga mellivora
James, Douglas, review by, 497–498
Jay, Blue, see Cyanocitta cristata
  Gray-breasted, see Aphelocoma ultramarina
  Steller's, see Cyanocitta stelleri
Johnson, Donald R., see Kennedy, Patricia L. and ———
Johnson, Ned K., review by, 616–625
Johnson, Rex R. and James J. Dinsmore, The use of tape-recorded calls to count Virginia Rails and Soras, 303–306
Junco, Dark-eyed, see Junco hyemalis
Junco hyemalis, 115, 214–230
Karr, James R., see Martin, Thomas E. and ———
Kennamer, Robert A., see Hoppe, Richard T. and ———
Kennedy, Patricia L. and Donald R. Johnson, Prey-size selection in nesting male and female Cooper's Hawks, 110–115
Kestrel, American, see Falco sparverius
Kibbe, Douglas P., see Laughlin, Sarah B. and ———
Kiff, Lloyd F., see Friedman, Herbert and ———
Killdeer, see Charadrius vociferus
King, Warren B., review by, 491–492
Kingbird, Eastern, see Tyrannus tyrannus
  Tropical, see Tyrannus melancholicus
Kingfisher, American Pygmy, see Chloroceryle aenea
Kinglet, Golden-crowned, see Regulus satrapa
  Ruby-crowned, see Regulus calendula
Kirk, Ethelyn L., see Graber, Jean W., Richard R. Graber, and ———
Kittiwake, Black-legged, see Rissa tridactyla
Kostin, Y. V., see Flint, V. E., R. L. Boehme, ———, and A. A. Kuznetzov
Kress, Stephen W., review by, 326
Kushlan, James A. and Paula C. Frohring, The history of the southern Florida Wood Stork population, 368–386
Kuznetzov, A. A., see Flint, V. E., R. L. Boehme, Y. V. Kostin, and ———
Laboudallon, Victorin, see Merritt, Robert E., Patricia A. Bell, and ———
Laboy, Eddie N., see Santana, Eduardo, C., ———, James A. Mosher, and Stanley A. Temple
Lack, Elizabeth, see Campbell, Bruce and ———
Lagopus lagopus albus, 597–600
  lagopus scoticus, 83
  leucurus, 427, 429, 597
Laniocera rufescens, 38–60
Lanius ludovicianus, 29
Lapwing, Southern, see Vanellus chilensis
Larus argentatus, 98, 101, 104, 157, 267–279, 297
  atricilla, 170–171
  californicus, 610–612, 615
  delawarensis, 101, 104, 107, 170–171, 267–279
  fuscus, 98
  philadelphia, 267–279
  spp., 25, 588–591
Laughlin, Sarah B. and Douglas P. Kibbe, eds., The atlas of breeding birds of Vermont, reviewed, 187–188
Leaftosser, Scaly-throated, see Sclerurus guatemalensis
Leberman, Robert C., review by, 621–622
Leck, Charles F., The status and distribution of New Jersey's birds, reviewed, 330–331
Lee, David S. and Gilbert S. Grant, An albino Greater Shearwater: feather abrasion and flight energetics, 488–490
Lee, David S., review by, 327
Lehmann, Val W., Bobwhites in the Rio Grande plain of Texas, reviewed, 492–493

Leptotila cassini, 38–60
verreauxi, 38–60
Lepus californicus, 446, 447, 450, 453
Levenson, Howard, see McGillivray, W. Bruce and ———
Limosa fedoa, 473–475
Lindauer, Martin, see Holldobler, Bert and ———
Littlefield, Carroll, D., Autumn Sandhill Crane habitat use in southeast Oregon, 131–137
lizard, alligator, see Gerrhonotus coeruleus
Lobipes lobatus, 588–591
Lombardo, Michael P., Extrapair copulations in the Tree Swallow, 150–152
Loon, Common, see Gavia immer
Lophodytes cucullatus, 167–168
Lophorina spp., 507
superba, 513
Lophospingus spp., 594–597
Løppenthin, Bernt, Johann Friedrich von Brandt: Icones avium Rossico-Americanarum. Tabulae VII, Ineditae, reviewed, 328–329
Lovejoy, T. E., see Diamond, A. W. and ———
Lumsden, Harry G., Judy Robinson, and Ronald Hartford, Choice of nest boxes by cavity-nesting ducks, 167–168
Lyons, David M., Kimberly Titus, and James A. Mosher, Sprig delivery by Broad-winged Hawks, 469–471
Lyrurus tetrix, 90
MacArthur, Patrick D., review by, 185–186
MacLean, Alexis A. E., Age-specific foraging ability and the evolution of deferred breeding in three species of gulls, 267–279
Maclean, Gordon Lindsay, Roberts' birds of southern Africa, reviewed, 179–181
Magpie, Black-billed, see Pica pica
Mallard, see Anas platyrhynchos
Manacus vitellinus, 38–60
Manakin, Blue-crowned, see Pipra coronata
Golden-collared, see Manacus vitellinus
Red-capped, see Pipra mentalis
Thrushlike, see Schiffornis turdinus
Manucodia jobiensis, 510
Manucode, Jobi, see Manucodia jobiensis
Margarops fuscatus, 126
Margolis, Carolyn, see Viola, Herman J. and ———
Marks, Jeffrey S., Nest-site characteristics and reproductive success of Long-eared Owls in southwestern Idaho, 547–560
Martin, Kathy, see Hik, David S., Susan J. Hannon, and ———
Martin, Purple, see Progne subis
Martin, Thomas E. and James R. Karr, Temporal dynamics of Neotropical birds with special reference to frugivores in second-growth woods, 38–60
McGillivray, W. Bruce and Howard Levenson, Distribution of food within broods of Barn Swallows, 286–291
McGowan, Kevin J. and Glen E. Woolfenden, Aerial rain bathing by Common Nighthawks, 612–613
McGuire, A. David, Some aspects of the breeding biology of Red-winged Blackbirds in Alaska, 257–266
Meanley, Brooke, The Marsh Hen, a natural history of the Clapper Rail of the Atlantic coast salt marsh, reviewed, 327–328
meetings and conferences
General Meeting of the Working Group on Granivorous Birds, INTECOL, 100
Proceeding of the sixty-seventh annual WOS meeting, 626–638
Third World Conference on Birds of Prey, 504
Megarhynchus pitangua, 38–60
Melanerpes erythrocephalus, 407–418
formicivorus, 284
pucherani, 38–60
Melanospiza spp., 594–597
Meleagris gallapavo, 158
Melopsittacus undulatus, 604
Melospiza georgiana, 604
melodia, 115, 231–242, 286
Mephitis mephitis, 158
Merganser, Common, see Mergus merganser
Hooded, see Lophodytes cucullatus
Mergus merganser, 167–168
Merlen, Godfrey, see Duffy, David Cameron and ———
Merlin, see Falco columbarius
Merritt, Robert E., Patricia A. Bell, and Victorin Laboudallon, Breeding biology of the Seychelles Black Parrot (Coracopsis nigra barklyi), 160–163

Michael, Edwin D., review by, 185
Micrathene whitneyi, 387–406
Micrastur semitorquatus, 38–60
Microeca flavovirescens, 511
Microrhopias quixensis, 38–60
Mimus polyglottos, 313–314
Mionectes oleagineus, 38–60
Mirarchi, Ralph E., see Hitchcock, Ronald R. and ———
Mniotilta varia, 38–60, 61–82, 163–167
Mockingbird, Northern, see Mimus polyglottos
Molothrus ater, 61–82, 214–230, 286, 459, 604
  bonariensis, 126–131
Momotus momota, 38–60
Monarch, Golden, see Monarcha chrysomela
Monarcha chrysomela, 510
Monroe, Burt L., Jr., review by, 499–500
Morris, Ralph D. and David A. Wiggins, Ruddy Turnstones, Great Horned Owls, and egg loss from Common Tern clutches, 101–109
Morrison, Michael L., Kimberly A. With, and Irene C. Timossi, The structure of a forest bird community during winter and summer, 214–230
Morton, E. S., see Buckley, P. A., M. S. Foster, ———, R. S. Ridgley, and F. G. Buckley
Morus spp., 607
Moseley, Carolyn, see Preston, Charles R., Hershel Moseley, and ———
Moseley, Hershel, see Preston, Charles, ———, and Carolyn Moseley
Mosher, James A., see Lyons, David M., Kimberly Titus, and ———
Mosher, James A., see Santana, Eduardo, C., Eddie N. Laboy, ———, and Stanley A. Temple
Motmot, Blue-crowned, see Momotus momota
  Rufous, see Baryphthengus ruficapillus
Mourner, Rufous, see Rhytipterna holerythra
  Speckled, see Laniocera rufescens
mouse, deer, see Peromyscus maniculatus
movement
  of juvenile Centrocercus urophasianus, 83–92
Mueller, Helmut C., The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors, 387–406
Murphy, Robert K., see Allen, George T., ———, Karen Steenhof, and Stephen W. Platt
Mustela erminea, 604
  spp., 298
Myadestes townsendi, 214–230
Mycteria americana, 368–386
Myers, J. P., review by, 175–176
Myiarchus crinitus, 38–60, 163–167, 321
  panamensis, 38–60
  tuberculifer, 38–60
Myiobius atricaudus, 38–60
Myiodynastes maculatus, 38–60
Myiozetetes similis, 38–60
Myospiza spp., 596
Myrmeciza exsul, 38–60
  longipes, 38–60
Myrmotherula axillaris, 38–60
  fulviventris, 38–60
  schisticolor, 343
Naranjo, Luis G., Aspects of the biology of the Horned Screamer in southwestern Colombia, 243–256
Nannopterum harrisi, 588
Neil, Wayne P., see Scotter, George W., ———, and J. David Henry
nest
  building by Buteo platypterus, 469–471
  cavity choice by ducks, 167–168
  characteristics of Buteo lineatus, 466–469
  construction by young Turdus migratorius, 319–320
  takeover by Eudocimus albus, 156–157
nesting
  in trees by Columba livia, 168–169
  record for Larus atricilla on Great Lakes, 170–171
  success of hummingbirds, 353–367
nestling
  growth rate
    of Agelaius phoeniceus, 257–266
    of Molothrus bonariensis and host nestlings, 126–131
    of Spizella breweri and Amphispiza belli, 535–546
nest site
  characteristics

in riparian habitat, 231–242
of Asio otus, 547–560
of Buteo jamaicensis in Puerto Rico, 561–570
selection
by Nycticorax nycticorax and Egretta thula, 300–303
use
of cattails by Egretta caerulea, 482–483
of fenceposts by Sialia sialis, 479–482
Netta rufina, 253
Nettleship, D. N., G. A. Sanger, and P. F. Springer, eds., Marine birds: their feeding ecology and commercial fisheries relationships, reviewed, 327
Newman, Kenneth, Birds of Southern Africa 1: Kruger National Park, reviewed, 621
Nighthawk, Common, see Chordeiles minor
Night-Heron, Black-crowned, see Nycticorax nycticorax
Noble, D. G., see Gaston, A. J., D. K. Cairns, R. D. Elliot, and ———
Noddy, Brown, see Anous stolidus
Norton, Robert L., see Schaffner, Fred C., ———, and John Taylor
Nuthatch, Red-breasted, see Sitta canadensis
White-breasted, see Sitta carolinensis
Nyctea scandiaca, 387–406
Nycticorax nycticorax, 101, 107, 108, 300–303, 476, 482
Nyctidromus albicollis, 38–60
Obst, Bryan S., Wax digestion in Wilson's Storm-Petrel, 189–195
Oceanites gracilis, 588–591
oceanicus, 189–195
spp., 588–591
Oceanodroma castro, 588–591
spp., 588–591
tethys, 588–591
O'Connor, Raymond J., The growth and development of birds, reviewed, 174–175
Odocoileus virginianus, 158, 600
Oncostoma olivaceum, 38–60
O'Neill, John P., review by, 182–183
O'Neill, John P., see Davis, Tristan J. and ———
O'Neill, John P., see Fitzpatrick, John W. and ———
Onychorhynchus mexicanus, 38–60
Oporornis formosus, 38–60, 163–167
philadelphia, 38–60
tolmiei, 214–230
opossum, Virginia, see Didelphis virginiana
Oreotrochilus estella, 365
Oriole, Hooded, see Icterus cucullatus
Northern, see Icterus galbula
Orchard, see Icterus spurius
Yellow-backed, see Icterus chrysater
Oropendola, Chestnut-headed, see Psarocolius wagleri
Ortalis cinereiceps, 38–60
Oryctolagus cuniculus, 115
Oryzoborus funereus, 38–60
spp., 594–597
Osprey, see Pandion haliaetus
Ostrich, see Struthio camelus
Ostrom, J. H., see Hecht, M. K., ———, G. Viohl, and P. Wellnhofer
Otus aequatorialis, see Otus ingens
asio, 387–406
clarkii, 9
colombianus, 1–14
flammeolus, 8, 12, 387–406
ingens, 1–14
kennicotti, 387–406
marshalli, 1–14
minimus, see Otus ingens
petersoni, 1–14 (Frontispiece)
scops, 387–406
trichopsis, 387–406
watsonii, 1–14
Ovenbird, see Seiurus aurocapillus
Ovis aries, 158
Owl, Barred, see Strix varia
Boreal, see Aegolius funereus
Burrowing, see Athene cunicularia
Elf, see Micrathene whitneyi
Flammulated, see Otus flammeolus
Great Gray, see Strix nebulosa
Great Horned, see Bubo virginianus
Little, see Athene noctua
Long-eared, see Asio otus
Northern Saw-whet, see Aegolius acadicus
Short-eared, see Asio flammeus
Snowy, see Nyctea scandiaca
Spotted, see Strix occidentalis
Tawny, see Strix aluco
Tengmalm's, see Aegolius funereus
Ural, see Strix uralensis

Page, Gary W., see Warriner, John S., Jane C. Warriner, ———, and Lynne E. Stenzel
Palmer, Ralph S., review by, 178–179
Pandion haliaetus, 117
Parabuteo unicinctus, 117
Paradisaea minor, 507, 509–510
spp., 507
Parakeet, Orange-chinned, see Brotogeris jugularis
parasitism
in sandpipers, 473–475
of Myiarchus crinitus nestling by larval fly, 321
Parker, Theodore A., see Hardy, John William and ———
Parkes, Kenneth C., reviews by, 323–324, 622–623
Parrot, Blue-headed, see Pionus menstruus
Puerto Rican, see Amazona vittata
Red-lored, see Amazona autumnalis
Seychelles Black, see Coracopsis nigra barklyi
Parula americana, 163–167
Parula, Northern, see Parula americana
Parus ater, 320
atricapillus, 61–82, 296, 312–313, 320–321, 407–418, 604
bicolor, 296
caeruleus, 320
carolinensis, 481
gambeli, 214–230, 321
major, 99, 320, 542
rufescens, 115, 214–230
Passer domesticus, 137–144, 287, 289–290, 602, 604, 614
montanus, 137
Passerculus sandwichensis, 321
Passerella iliaca, 214–230
Passerina ciris, 163–167
cyanea, 38–60, 61–82, 163–167, 231–242, 284
Pauraque, Common, see Nyctidromus albicollis
Payne, Robert B., review by, 179–181, 181–182
Pelecanus occidentalis, 588–591
Pelican, Brown, see Pelecanus occidentalis
Penguin, Galapagos, see Spheniscus mendiculus
Peromyscus maniculatus, 115
Perrins, C. M. and T. R. Birkhead, Avian ecology, reviewed, 173–174
Petersen, Kenneth L., Louis B. Best, and Brian M. Winter, Growth of nestling Sage Sparrows and Brewer's Sparrows, 535–546
Peterson, A. Townsend, Rock Doves nesting in trees, 168–169
Petrel, Dark-rumped, see Pterodroma phaeopygia
Phaenostictus mcleannani, 38–60
Phaethon aethereus, 588–591
Phaethornis longuemareus, 38–60
superciliosus, 38–60
Phalacrocorax albiventer, 571–580
albiventer purpurascens, 578
atriceps, 571–580
olivaceus, 607–608
Phalarope, Northern, see Lobipes lobatus
Red, see Phalaropus fulicaria
Red-necked, see Phalaropus lobatus
Wilson's, see Phalaropus tricolor
Phalaropus fulicaria, 35
lobatus, 35
tricolor, 473–475, 608
Pharomachrus mocinno, 587
Phasianus colchicus, 598
Pheasant, Ring-necked, see Phasianus colchicus
Pheucticus ludovicianus, 38–60, 163–167, 196–213, 231–242
melanocephalus, 214–230, 486–488
Phillips, J. G., P. J. Butler, and P. J. Sharp, Physiological strategies in avian biology, reviewed, 619–621
Piaya cayana, 38–60
Pica pica, 548
Picman, Jaroslav, see Belles-Isles, Jean-Claude and ———
Picoides albolarvatus, 214–230
pubescens, 61–82, 211, 214–230, 319
villosus, 214–230
Pierson, Thomas A. and Patrick F. Scanlon, Use of fencepost cavities by nesting Eastern Bluebirds in southwestern Virginia, 479–482
pig, see Sus scrofa
Pigeon, Band-tailed, see Columba fasciata
Purple-crowned, see Ducula spilorrhoa
Scaled, see Columba speciosa

White-crowned, see Columba leucocephala
Wood, see Columba palumbus
Pionus menstruus, 38–60
Pipilo erythrophthalmus, 61–82, 115, 214–230
spp., 596
Pipra coronata, 38–60
mentalis, 38–60
Piranga ludoviciana, 214–230
olivacea, 196–213
rubra, 38–60, 163–167, 364
Pitohui ferrugineus, 508, 510
kirhocephalus, 510
Pitohui, Rusty, see Pitohui ferrugineus
Variable, see Pitohui kirhocephalus
Pituophis melanoleucus, 553
Platt, Stephen W., see Allen, George T., Robert K. Murphy, Karen Steenhof, and ———
Platyrinchus coronatus, 38–60
Plover, Mountain, see Charadrius montanus
Piping, see Charadrius melodus
Snowy, see Charadrius alexandrinus
Wilson's, see Charadrius wilsonia
Plumeleteer, White-vented, see Chalybura buffonii
Pochard, see Aythya ferina
Red-crested, see Netta rufina
Podargus sp., 613
Polioptila plumbea, 38–60
polygyny
in Coccothraustes vespertinus, 308
in Dendroica petechia, 152–154, 315–317
Pomatostomus isidorei, 508, 510
Pooecetes gramineus, 144–147, 321
population
dynamics of mast-eating species in eastern United States, 407–418
history of Mycteria americana in southern Florida, 368–386
temporal dynamics of Neotropical birds, 38–60
Porzana carolina, 303–306
Prairie-Chicken, Greater, see Tympanuchus cupido pinnatus
Prasad, N. L. N. S. and Fred S. Guthery, Drinking by Northern Bobwhites in Texas, 485–486
predation
of Charadrius vociferus by Vulpes vulpes, 605–607
on Coragyps atratus and Cathartes aura, 600–601
on nests of Sialia sialis by Elaphe obsoleta obsoleta, 602–603
Preston, Charles R., Hershel Moseley, and Carolyn Moseley, Green-backed Heron baits fish with insects, 613–614
Procyon lotor, 298, 553, 604
productivity
of hummingbirds, 353–367
Progne subis, 151, 483
Protonotaria citrea, 38–60, 163–167
Psarocolius wagleri, 38–60
Ptarmigan, White-tailed, see Lagopus leucurus
Willow, see Lagopus lagopus albus
Pterodroma phaeopygia, 588–591
Pteroglossus torquatus, 38–60
Ptiloris magnificus, 508–510
spp., 507
Puffbird, White-necked, see Bucco macrorhynchus
Puffin, Tufted, see Fratercula cirrhata
Puffinus gravis, 488–490
lherminieri, 588–591
Pugesek, Bruce and Kenneth L. Diem, Ages of mated pairs of California Gulls, 610–612
Pygmy-Owl, European, see Glaucidium passerinum
Ferruginous, see Glaucidium brasilianum
Northern, see Glaucidium gnoma
Pygmy-Tyrant, Cinnamon-breasted, see Hemitriccus cinnamomeipectus
Quail, Blue-breasted, see Coturnix chinensis
California, see Callipepla californica
Common, see Coturnix coturnix
Quay, W. B., Timing and location of spring sperm release in northern thrushes, 526–534
Querula purpurata, 38–60
Quetzal, Resplendent, see Pharomachrus mocinno
Quinney, Terry E., Male and female parental care in Tree Swallows, 147–150
Quiscalus major, 615

mexicanus, 614–615
niger, 126–131
quiscula, 299, 604, 614
rabbit, black-tailed jack, see Lepus californicus
domestic, see Oryctolagus cuniculus
raccoon, see Procyon lotor
Raikow, Robert J., reviews by, 331, 618–619
Rail, Virginia, see Rallus limicola
Rallus limicola, 303–306
Ramphastos sulfuratus, 38–60
Ramphocaenus melanurus, 38–60
Ramphocelus melanurus, 38–60
icteronotus, 38–60
range extension
of Sterna sandvicensis eurygnatha, 317–318
Raphael, Martin G. and Marshall White, Use of snags by cavity-nesting birds in the Sierra Nevada, reviewed, 494–495
Rasmussen, Pamela C., Nest-building behavior in a young American Robin, 319–320
rat, Norway, see Rattus norvegicus
sp., see Rattus rattus and Rattus sp.
Rattus norvegicus, 158
rattus, 163
sp., 115
Raven, Common, see Corvus corax
Rayner, Jeremy M. V., Vertebrate flight: a bibliography to 1985, reviewed, 502
Razorbill, see Alca torda
Recurvirostra americana, 29, 474
Redhead, see Aythya americana
Redstart, American, see Setophaga ruticilla
Reed, J. Michael, Vegetation structure and Vesper Sparrow territory location, 144–147
Regulus calendula, 214–230
satrapa, 214–230
Reid, Mary L. and Spencer G. Sealy, Behavior of a polygynous yearling Yellow Warbler, 315–317
reproductive success
of Asio otus, 547–560
Reynard, George B., review by, 330–331
Rhipidura rufidorsa, 511
Rhynchocyclus olivaceus, 38–60
Rhytipterna holerythra, 38–60
Ridgley, R. S., see Buckley, P. A., M. S. Foster, E. S. Morton, ———, and F. G. Buckley
Riflebird, Magnificent, see Ptiloris magnificus
Riley, Cecilia M., Observations on the breeding biology of Emerald Toucanets in Costa Rica, 585–588
Riparia riparia, 150, 286, 483–484, 608
Ripley, S. Dillon and Bruce M. Beehler, Rails of the world, a compilation of new information, 1975–1983 (Aves: Rallidae), reviewed, 503
Rissa tridactyla, 99
Robin, American, see Turdus migratorius
Clay-colored, see Turdus grayi
Robinson, Judy, see Lumsden, Harry G., ———, and Ronald Hartford
Rógel, Antonio, B., see Rogers, David T., Jr., Jesús Garcia B., and ———
Rogers, David T., Jr., Jésus Garcia B., and Antonio Rógel B., Additions to records of North American avifauna in Yucatán, Mexico, 163–167
Saltator albicollis, 38–60
maximus, 38–60
Saltator, Buff-throated, see Saltator maximus
Streaked, see Saltator albicollis
Samson, Jack, Modern falconry, reviewed, 186
Sandpiper, Spotted, see Actitis macularia
Upland, see Bartramia longicauda
Sanger, G. A., see Nettleship, D. N., ———, and P. F. Springer
Santana, Eduardo, C., Eddie N. Laboy, James A. Mosher, and Stanley A. Temple, Red-tailed Hawk nest sites in Puerto Rico, 561–570
Sapsucker, Red-breasted, see Sphyrapicus ruber
Scanlon, Patrick F., sec Pierson, Thomas A. and ———
Scaup, Greater, sec Aythya marila
Lesser, see Aythya affinis
Schaffner, Fred C., Robert L. Norton, and John Taylor, range extension of Cay-

enne Terns on the Puerto Rico Bank, 317–318
Schiffornis turdinus, 38–60
Schnell, Gary, see Wood, D. Scott and ———
Schuchmann, Karl-L., ed., African vertebrates: systematics, phylogeny, and evolutionary biology, reviewed, 499–500
Schwab, Larry, review by, 621
Sciurus carolinensis, 158
Sclerurus guatemalensis, 38–60
Scops-Owl, European, see Otus scops
Scott, Thomas C., Bobwhite thesaurus, reviewed, 185
Scotter, George W., Wayne P. Neil, and J. David Henry, Birds of Nahanni National Park, Northwest Territories, reviewed, 188
Screamer, Horned, see Anhima cornuta
Northern, see Chauna chavaria
Southern, see Chauna torquata
Screech-Owl, Eastern, see Otus asio
Western, see Otus kennicotti
Whiskered, see Otus trichopis
Sealy, Spencer G., see Reid, Mary L. and ———
seasonal dynamics of avian communities, 61–82
Seedeater, Variable, see Sporophila aurita
Seed-Finch, Thick-billed, see Oryzoborus funereus
Seiurus aurocapillus, 38–60, 61–82, 163–167
noveboracensis, 38–60, 163–167
Selasphorus platycercus, 354
Seleucidis melanoleuca, 507, 510
Setophaga ruticilla, 163–167, 196–213
sexual dimorphism
of owls, 387–406
of Sterna hirundo, 93–100
Shag, Emperor, see Phalacrocorax albiventer purpurascens
Imperial Blue-eyed, see Phalacrocorax atriceps
King, see Phalacrocorax albiventer
Shallenberger, Robert J., ed., Hawaii's birds, reviewed, 331
Sharp, P. J., see Phillips, J. G., P. J. Butler, and ———
Shearwater, Audubon's, see Puffinus lherminieri
Cory's, see Calonectris diomedea
Greater, see Puffinus gravis
sheep, see Ovis aries
Shields, Mark A., see Frederick, Peter C. and ———
Shrike, Loggerhead, see Lanius ludovicianus
Sialia mexicana, 214–230
sialis, 479–482, 486, 602–603
Sicalis spp., 595
Sicklebill, Brown, see Epimachus meyeri
Buff-tailed, see Epimachus albertisi
Pale-billed, see Epimachus bruijnii
Siegel-Causey, Douglas, The courtship behavior and mixed-species pairing of King and Imperial Blue-eyed Shags (Phalacrocorax albiventer and P. atriceps), 571–580
Simons, Lee H., Adult male Blue Grouse eats lizards, 171–172
Siskin, Pine, see Carduelis pinus
Sitta canadensis, 115, 214–230
carolinensis, 64, 66, 296
skunk, striped, see Mephitis mephitis
Smith, Jeffrey K., see Cody, Ronald P. and ———
Smith, Kimberly G., Brown Thrashers respond to calls of Northern Mockingbird nestlings, 313–314
Smith, Kimberly G., see Hensley, R. Craig and ———
Smith, Kimberly G., Winter population dynamics of three species of mast-eating birds in the eastern United States, 407–418
Smith, Loren M., see Bergan, James F., and ———
snake, black rat, see Elaphe obsoleta obsoleta
bull, see Pituophis melanoleucus
Snipe, Common, see Gallinago gallinago
social organization
of Dendragapus obscurus, 419–432
Solitaire, Townsend's, see Myadestes townsendi
Sora, see Porzana carolina
Souza, Richard, see Strong, Paul I. V., John A. Bissonette, and ———
Spadebill, Golden-crowned, see Platyrinchus coronatus
Sparrow, Black-striped, see Arremonops conirostris
Brewer's, see Spizella breweri

Cape Sable Seaside, see Ammodramus maritimus
Chipping, see Spizella passerina
European Tree, see Passer montanus
Field, see Spizella pusilla
Fox, see Passerella iliaca
Grasshopper, see Ammodramus savannarum
Grassland, see Ammodramus humeralis
House, see Passer domesticus
Sage, see Amphispiza belli
Savannah, see Passerculus sandwichensis
Song, see Melospiza melodia
Swamp, see Melospiza georgiana
Vesper, see Pooecetes gramineus
White-crowned, see Zonotrichia leucophrys
White-throated, see Zonotrichia albicollis
Yellow-browed, see Ammodramus aurifrons
Sparrowhawk, European, see Accipiter nisus
species-area relationship
of migrants in woodlots, 291–296
sperm release
in northern thrushes, 526–534
Spheniscus mendiculus, 588–591
Sphyrapicus ruber, 214–230
Spiza americana, 614
Spizella breweri, 535–546
passerina, 61–82, 321
pusilla, 61–82, 286
Sporophila ardesiaca, 594–597
aurita, 38–60
cinnamomea, 594–597
frontalis, 594–597
insulata, 594–597
melanops, 594–597
nigrorufa, 594–597
obscura, 594–597
palustris, 594–597
spp., 594–597
Springer, P. F., see Nettleship, D. N., G. A. Singer, and ———
squirrel, gray, see Sciurus carolinensis
red, see Tamiasciurus hudsonicus
Stafford, Michael, D., Supernumerary adults feeding Willow Flycatcher fledglings, 311–312
Starling, European, see Sturnus vulgaris
Stauffer, Dean F. and Louis B. Best, Nest-site characteristics of open-nesting birds in riparian habitats in Iowa, 231–242
Stauffer, Dean F., see Garrison, Barrett A., Catherine Vouchilas, and ———
Stedman, Stephen J., see Vogt, David F., C. Gerald Drewry, Paul B. Hamel, and ———
Steenhof, Karen, see Allen, George T., Robert K. Murphy, ———, and Stephen W. Platt
Stelgidopteryx serripennis, 483
Stenzel, Lynne E., see Warriner, John S., Jane C. Warriner, Gary W. Page, and ———
Sterna fuscata, 108
hirundo, 93–100, 101–109, 610
lunata, 108
maxima, 317
sandvicensis acuflavida, 317–318
sandvicensis eurygnatha, 317–318
Stiles, F. Gary and Pedro G. Aguilar F., eds., Primer symposio de ornitologia Neotropical, reviewed, 323–324
Stint, Temminck's, see Calidris temminckii
Stork, Maguari, see Euxenura maguari
Wood, see Mycteria americana
Storm, Gerald L., see Yahner, Richard H., ———, and Anthony L. Wright
Storm-Petrel, Band-rumped, see Oceanodroma castro
Wedge-rumped, see Oceanodroma tethys
White-vented, see Oceanites gracilis
Wilson's, see Oceanites oceanicus
Streptopelia risoria, 297
Strix aluco, 387–406
nebulosa, 387–406
occidentalis, 387–406
uralensis, 387–406
varia, 387–406
Strong, Paul I. V., John A. Bissonette, and Richard Souza, A case of brood mixing by Common Loons, 478–479
Struthio camelus, 297
Sturnus vulgaris, 115, 481
Sula dactylatra, 588–591
nebouxii, 588–591
Sunangel, Royal, see Heliangelus regalis
Surnia ulula, 387–406
survival
of muscle-biopsied Zonotrichia albicollis, 280–285

Sus scrofa, 158
Sutton, George Miksch, Eskimo year, reviewed, 329–330
Swallow, Bank, see Riparia riparia
  Barn, see Hirundo rustica
  Cliff, see Hirundo pyrrhonota
  Northern Rough-winged, see Stelgidopteryx serripennis
  Tree, see Tachycineta bicolor
  Violet-green, see Tachycineta thalassina
Sylvilagus floridanus, 158
systematics
  of foot-scute patterns in Neotropical finches, 594–597
Tachycineta bicolor, 126, 147–150, 150–152, 483–484, 487
  thalassina, 483–484
Tachyphonus luctuosus, 38–60
  rufus, 38–60
Tamias striatus, 210, 298
  townsendi, 115
Tamiasciurus hudsonicus, 604
Tanager, Blue-gray, see Thraupis episcopus
  Crimson-backed, see Ramphocelus dimidiatus
  Golden-masked, see Tangara larvata
  Gray-headed, see Eucometis penicillata
  Plain-colored, see Tangara inornata
  Scarlet, see Piranga olivacea
  Summer, see Piranga rubra
  Western, see Piranga ludoviciana
  White-lined, see Tachyphonus rufus
  White-shouldered, see Tachyphonus luctuosus
  Yellow-rumped, see Ramphocelus icteronotus
Tangara larvata, 38–60
  inornata, 38–60
taxonomy
  of Aythya group (scaup), 433–444
  of Herpsilochmus group, 337–353
  of Otus petersoni, 1–14
  of Otus group, 1–14
Taylor, John, see Schaffner, Fred C., Robert L. Norton, and ———
Teal, Green-winged, see Anas crecca
technique
  muscle biopsy of Zonotrichia albicollis, 280–285
  use of tape-recorded calls to count Rallus limicola and Porzana carolina, 303–306
Temple, Stanley A., see Santana, Eduardo, C., Eddie N. Laboy, James A. Mosher, and ———
Terenotriccus erythrurus, 38–60
Tern, Cayenne, see Sterna sandvicensis eurygnatha
  Common, see Sterna hirundo
  Gray-backed, see Sterna lunata
  Royal, see Sterna maxima
  Sandwich, see Sterna sandvicensis acuflavida
  Sooty, see Sterna fuscata
Tetroa tetrix, 425
  urogallus, 425
Thamnophilus punctatus, 38–60
Thrasher, Brown, see Toxostoma rufum
  Pearly-eyed, see Margarops fuscatus
Thraupis episcopus, 38–60
Thrush, Gray-cheeked, see Catharus minimus
  Hermit, see Catharus guttatus
  Mistle, see Turdus viscivorus
  Swainson's, see Catharus ustulatus
  Varied, see Ixoreus naevius
  Wood, see Hylocichla mustelina
Thryothorus fasciatoventris, 38–60
  modestus, 38–60
  nigricapillus, 38–60
Tiaris spp., 594–597
Tiebout, Harry M., III, Downy Woodpecker feeds on insects in a spider's web, 319
Timossi, Irene C., see Morrison, Michael L., Kimberly A. With, and ———
Tinamou, Little, see Crypturellus soui
Tit, Blue, see Parus caeruleus
  Coal, see Parus ater
  Great, see Parus major
Titmouse, Tufted, see Parus bicolor
Titus, Kimberly, see Lyons, David M., ———, and James A. Mosher
Tityra, Black-crowned, see Tityra inquisitor
  Masked, see Tityra semifasciata
Tityra inquisitor, 38–60
  semifasciata, 38–60
Toland, Brian, Hunting success of some Missouri raptors, 116–125

Tomback, Diana F., review by, 324–326
Toucan, Keel-billed, see Ramphastos sulfuratus
Toucanet, Emerald, see Aulacorhynchus prasinus
Towhee, Rufous-sided, see Pipilo erythrophthalmus
Toxostoma rufum, 231–242, 313–314
Tramer, Elliot J. and Louis W. Campbell, Laughing Gull nesting attempt on Lake Erie, 170–171
Troglodytes aedon, 481, 604
  troglodytes, 214–230
Trogon massena, 38–60
  violaceus, 38–60
  viridis, 38–60
Trogon, Slaty-tailed, see Trogon massena
  Violaceous, see Trogon violaceus
  White-tailed, see Trogon viridis
Tropic-bird, Red-billed, see Phaethon aethereus
Tunnicliffe, C. F., Tunnicliffe's birds, measured drawings, reviewed, 182–183
Turdus grayi, 38–60
  migratorius, 110, 111, 214–230, 231–242, 319–320, 604, 615
  viscivorus, 320
turkey, domestic, see Meleagris gallapavo
Turnstone, Ruddy, see Arenaria interpres
Turtle-Dove, Ringed, see Streptopelia risoria
Tympanuchus cupido pinnatus, 83, 598
  phasianellus, 91, 427, 429
Tyrannus melancholicus, 38–60
  tyrannus, 38–60
Tyrell, Esther Q., Hummingbirds: their life and behavior, reviewed, 183–185
Tyto alba, 387–406
Van Der Raay, B. M., see Campbell, R. W., E. D. Forsman, and ———
Vanellus chilensis, 253
Veery, see Catharus fuscescens
Vermivora chrysoptera, 38–60, 61–82
  peregrina, 38–60, 163–167
  pinus, 38–60, 163–167
  pinus × chrysoptera, 163–167
  ruficapilla, 61–82, 214–230
Viohl, G., see Hecht, M. K., J. H. Ostrom, ———, and P. Wellnhofer
Viola, Herman J. and Carolyn Margolis, eds., Magnificent voyagers, reviewed, 501–502
Vireo flavifrons, 38–60
  flavoviridis, 38–60
  gilvus, 214–230
  griseus, 163–167
  huttoni, 115
  olivaceus, 38–60, 61–82, 163–167, 196–213
  philadelphicus, 196–213
  solitarius, 214–230
  sp., 115
Vireo, Hutton's, see Vireo huttoni
  Philadelphia, see Vireo philadelphicus
  Red-eyed, see Vireo olivaceus
  Solitary, see Vireo solitarius
  Warbling, see Vireo gilvus
  White-eyed, see Vireo griseus
  Yellow-green, see Vireo flavoviridis
  Yellow-throated, see Vireo flavifrons
vocalization
  of Epimachus bruijnii, 509, 512
  Toxostoma rufum response to nestling Mimus polyglottus distress calls, 313–314
Vogt, David F., C. Gerald Drewry, Paul B. Hamel, and Stephen J. Stedman, Birds of the Nashville area, reviewed, 332
Volatinia jacarina, 38–60
  spp., 594–597
Vouchilas, Catherine, see Garrison, Barrett A., ———, and Dean F. Stauffer
Vulpes vulpes, 158, 605–606
Vulture, Black, see Coragyps atratus
  Turkey, see Cathartes aura
Warbler, Bay-breasted, see Dendroica castanea
  Black-and-white, see Mniotilta varia
  Blackburnian, see Dendroica fusca
  Black-throated Blue, see Dendroica caerulescens
  Black-throated Green, see Dendroica virens
  Blue-winged, see Vermivora pinus
  Chestnut-sided, see Dendroica pensylvanica
  Golden-winged, see Vermivora chrysoptera

Hermit, see Dendroica occidentalis
Hooded, see Wilsonia citrina
Kentucky, see Oporornis formosus
Lawrence's, see Vermivora pinus × chrysoptera
MacGillivray's, see Oporornis tolmiei
Magnolia, see Dendroica magnolia
Mourning, see Oporornis philadelphia
Nashville, see Vermivora ruficapilla
Palm, see Dendroica palmarum
Prairie, see Dendroica discolor
Prothonotary, see Protonotaria citrea
Tennessee, see Vermivora peregrina
Wilson's, see Wilsonia pusilla
Yellow, see Dendroica petechia
Yellow-rumped, see Dendroica coronata
Yellow-throated, see Dendroica dominica
Wakeley, James S., see Gavett, Ann P. and ———
Warriner, Jane C., see Warriner, John S., ———, Gary W. Page, and Lynne E. Stenzel
Warriner, John S., Jane C. Warriner, Gary W. Page, and Lynne E. Stenzel, Mating system and reproductive success of a small population of polygamous Snowy Plovers, 15–37
Waterthrush, Northern, see Seiurus noveboracensis
Waxwing, Cedar, see Bombycilla cedrorum
weasel, see Mustela spp.
short-tailed, see Mustela erminea
Weise, Charles M., see Apel, Karen M. and ———
Wellnhofer, P., see Hecht, M. K., J. H. Ostrom, G. Viohl, and ———
Werden, Allan H., review by, 177–178
Westmoreland, David and Louis B. Best, Incubation continuity and the advantage of cryptic egg coloration to Mourning Doves, 297–300
Westneat, David F., The effects of muscle biopsy on survival and condition in White-throated Sparrows, 280–285
White, Clayton M., review by, 186
White, Marshall, see Raphael, Martin G. and ———
Whitmore, Robert C., reviews by, 173–174, 494–495, 497
Wigeon, American, see Anas americana
Wiggins, David A., see Morris, Ralph D. and ———
Wiley, James W., Growth of Shiny Cowbirds and host chicks, 126–131
Willet, Western, see Catoptrophorus semipalmatus
Wilson, Marie-Pierre, see Duffy, David Cameron, Rory P. Wilson, and ———
Wilson, Rory P., see Duffy, David Cameron, ———, and Marie-Pierre Wilson
Wilsonia citrina, 163–167
pusilla, 321
Winter, Brian M., see Petersen, Kenneth L., Louis B. Best, and ———
With, Kimberly A., see Morrison, Michael L., ———, and Irene C. Timossi
Wolfe, Larry L., review by, 183–185
Wood, D. Scott and Gary D. Schnell, Distribution of Oklahoma birds, reviewed, 497–498
Wood, D. Scott, reviews by, 328–329, 329–330
Woodcreeper, Buff-throated, see Xiphorhynchus guttatus
Plain-brown, see Dendrocincla fuliginosa
Ruddy, see Dendrocincla homochroa
Wedge-billed, see Glyphorhynchus spirurus
Woodpecker, Acorn, see Melanerpes formicivorus
Black-cheeked, see Melanerpes pucherani
Downy, see Picoides pubescens
Hairy, see Picoides villosus
Lineated, see Dryocopus lineatus
Pileated, see Dryocopus pileatus
Red-headed, see Melanerpes erythrocephalus
White-headed, see Picoides albolarvatus
Wood-Pewee, Eastern, see Contopus virens
Western, see Contopus sordidulus
Woodrey, Mark S., Characteristics of Red-shouldered Hawk nests in southeast Ohio, 466–469
Wood-Wren, Bar-winged, see Henicorhina leucoptera
White-breasted, see Henicorhina leucosticta
Woolfenden, Glen E. and John W. Fitzpatrick, The Florida Scrub Jay: demog-

raphy of a cooperative breeding bird, reviewed, 324–326
Woolfenden, Glen E., see McGowan, Kevin J. and ———
Wootton, J. Timothy, Clutch-size differences in western and introduced eastern populations of House Finches: patterns and hypotheses, 459–462
Wootton, J. Timothy, see Bollinger, Eric K., Thomas A. Gavin, Catherine J. Hibbard, and ———
Wren, Bay, see Thryothorus nigricapillus
Black-bellied, see Thryothorus fasciatoventris
House, see Troglodytes aedon
Marsh, see Cistothorus palustris
Plain, see Thryothorus modestus
Sedge, see Cistothorus platensis
Song, see Cyphorhinus phaeocephalus
Winter, see Troglodytes troglodytes
Wright, Anthony L., see Yahner, Richard H., Gerald L. Storm, and ———
Xenops minutus, 38–60
rutilans, 343
Xenops, Plain, see Xenops minutus
Streaked, see Xenops rutilans
Xiphorhynchus guttatus, 38–60
ocellatus, 343
Yahner, Richard H., Gerald L. Storm, and Anthony L. Wright, Winter diets of vultures in southcentral Pennsylvania, 157–160
Yahner, Richard H., Structure, seasonal dynamics, and habitat relationships of avian communities in small even-aged forest stands, 61–82
Yellowthroat, Common, see Geothlypis trichas
Zenaida asiatica, 310, 582
macroura, 115, 231–242, 297–300, 309–311, 581–585, 602
Zonotrichia albicollis, 280–285
leucophrys, 115
spp., 596

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*Editor* Keith L. Bildstein
Department of Biology
Winthrop College
Rock Hill
South Carolina 29733

*Associate Editors* Michael W. Collopy
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*Review Editor* George A. Hall
Department of Chemistry
P.O. Box 6045
West Virginia University
Morgantown, WV 26506

*Color Plate Editor* William A. Lunk
865 North Wagner
Road
Ann Arbor, MI 48103

*Index Editor* Kathy G. Beal
616 Xenia Avenue
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## CONTENTS


OBSERVATIONS ON THE ECOLOGY AND BEHAVIOR OF THE PALE-BILLED SICKLEBILL
*Bruce M. Beehler and Carol H. Beehler* 505

POTENTIAL USE OF FEATHER CHEMISTRY AS AN INDICATOR OF RELATIVE GROWTH
*Gary R. Bortolotti and Jon C. Barlow* 516

TIMING AND LOCATION OF SPRING SPERM RELEASE IN NORTHERN THRUSHES ..... *W. B. Quay* 526

GROWTH OF NESTLING SAGE SPARROWS AND BREWER'S SPARROWS
*Kenneth L. Petersen, Louis B. Best, and Brian M. Winter* 535

NEST-SITE CHARACTERISTICS AND REPRODUCTIVE SUCCESS OF LONG-EARED OWLS IN SOUTHWESTERN IDAHO ..... *Jeffrey S. Marks* 547

RED-TAILED HAWK NEST SITES IN PUERTO RICO
*Eduardo Santana C., Eddie N. Laboy, James A. Mosher, and Stanley A. Temple* 561

THE COURTSHIP BEHAVIOR AND MIXED-SPECIES PAIRING OF KING AND IMPERIAL BLUE-EYED SHAGS (*PHALACROCORAX ALBIVENTER* AND *P. ATRICEPS*) ..... *Douglas Siegel-Causey* 571

GENERAL NOTES

DISPERSAL OF RECENTLY FLEDGED MOURNING DOVES FROM NEST SITES
*Ronald R. Hitchcock and Ralph E. Mirarchi* 581

OBSERVATIONS ON THE BREEDING BIOLOGY OF EMERALD TOUCANETS IN COSTA RICA
*Cecilia M. Riley* 585

SEABIRD DENSITIES AND AGGREGATIONS DURING THE 1983 EL NIÑO IN THE GALAPAGOS ISLANDS ..... *David Cameron Duffy and Godfrey Merlen* 588

COLOR VARIATION IN THE RUDDY DUCK (*OXYURA JAMAICENSIS ANDINA*) ..... *Jon Fjeldså* 592

SYSTEMATIC INTERPRETATIONS OF FOOT-SCUTE PATTERNS IN NEOTROPICAL FINCHES
*George A. Clark, Jr.* 594

NORTHERN HARRIER PREDATION ON WILLOW PTARMIGAN
*David S. Hik, Susan J. Hannon, and Kathy Martin* 597

PREDATION ON BLACK AND TURKEY VULTURES .... *John S. Coleman and James D. Fraser* 600

EASTERN BLUEBIRD RESPONSES TO NOCTURNAL BLACK RAT SNAKE PREDATION
*R. Craig Hensley and Kimberly G. Smith* 602

DESTRUCTION OF HETEROSPECIFIC EGGS BY THE GRAY CATBIRD
*Jean-Claude Belles-Isles and Jaroslav Picman* 603

FATAL ANTIPREDATOR BEHAVIOR OF A KILLDEER ..... *Dianne H. Brunton* 605

PLUNGE-DIVING BY OLIVACEOUS CORMORANTS IN CHILE ..... *David Cameron Duffy, Rory P. Wilson, Marie-Pierre Wilson, and Claudio Velasquez R.* 607

WHICH SEX LEADS IN PAIRED MALLARDS? ..... *Kim C. Derrickson* 608

AGES OF MATED PAIRS OF CALIFORNIA GULLS ..... *Bruce H. Pugesek and Kenneth L. Diem* 610

AERIAL RAIN BATHING BY COMMON NIGHTHAWKS
*Kevin J. McGowan and Glen E. Woolfenden* 612

GREEN-BACKED HERON BAITS FISH WITH INSECTS
*Charles R. Preston, Hershel Moseley, and Carolyn Moseley* 613

GREAT-TAILED GRACKLE KILLS BARN SWALLOW IN FLIGHT ..... *Roger B. Clapp* 614

ORNITHOLOGICAL LITERATURE ..... 616

PROCEEDINGS OF THE SIXTY-SEVENTH ANNUAL MEETING ..... *John L. Zimmerman* 626

ANNOUNCEMENTS ..... 534, 560, 625, 639

INDEX ..... 641

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